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POUR L'EXPLORATION DE LA MER
CHARLOTTENLUND SLOT – DANEMARK

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J. R. LUMBY

EN COMMISSION CHEZ
ANDR. FRED. HØST & FILS
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MAI 1953

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IMPRIMERIE A/S L. IHRICH . COPENHAGEN

Studies on Plankton Populations.

By

D. H. Cushing,

Fisheries Laboratory, Lowestoft.

Introduction.

The fisheries on herring in the summer-time are concentrated by the aggregation of the fish shoals on to patches of their food. This aggregation has been the basis of much work on the *Calanus* — herring relation, including especially that of Hardy *et al.* (1936), Savage (1937), and Manteufel (1941). An assumption in the earlier work was that a high density of *Calanus* was related to a high catch of herring; as work proceeded, it became clear that negative associations between *Calanus* and herring were possible, as well as positive ones. It seemed possible from a review of this literature that the whole relation might depend upon three main factors; firstly, the aggregation of herring on to their food patches; secondly, the *Calanus* mortality due to herring grazing, and thirdly, the recruitment of the larger stages of *Calanus* into the system. The second and third factors would work against each other, the second dominating the system until the numbers of *Calanus* sharply decrease and the herring disengaged.

At this point, it became clear that the whole production cycle, from the use of phosphorus by the plants to the searching for the herring shoals by the drifters, was relevant to the problem. The five methods to be described in this paper are the basis of a possible dynamic description of this production cycle.

The Separation of Contour Levels.

It is well known that plankton organisms occur in patches and the arrangement of the grid of stations on these cruises ensured that certain patches were described. Plants and animals were entered on the charts for each cruise, using the numbers underneath 1 m^2. of the sea surface. It was then necessary to draw contours from which to estimate the numbers in each patch. Contour levels should be chosen far enough apart to make unlikely the inclusion of a sample between two contour levels that, according to statistical canons, should derive from a population value outside these levels. In order to obtain such a standard for the plankton animals on which I was working, I had recourse to some of Mr. A. C. Simpson's data of plankton taken on plaice-egg

Table 1.
Derivation of confidence limits for the separation of contours.

Cruise I. "Sir Lancelot", 1949.

		Paracalanus parvus Mean Squares			*Pseudocalanus elongatus* Mean Squares		
	DF	M	F	Juv.	M	F	Juv.
Nets	2	0·0013	0·4065	0·0600	0·1125	0·1190	0·9830
Stations	21	0·0559	0·2349	0·4036	0·2407	0·5404	0·5830
Error	42	0·0280	0·1800	0·1039	0·0897	0·1133	0·1480
Residual	44	0·0268	0·1900	0·1020	0·0908	0·1140	0·1860
Sq. Rt. Resid.		0·1637	0·4359	0·3194	0·3013	0·3376	0·4313
$\times t_{DF}$ p 0·05		0·3208	0·8543	0·6260	0·5905	0·6617	0·8453
Antilog		2·093	7·150	4·227	3·895	4·588	7·003

Cruise II. "Sir Lancelot", 1949.

		Paracalanus parvus Mean squares			*Pseudocalanus elongatus* Mean Squares			*Temora*
	DF	M	F	Juv.	M	F	Juv.	
Net	2	0·0578	0·0569	0·1794	0·0488	0·0117	0·2002	0·1791
Stations	36	0·0827	0·8063	0·7250	0·0940	0·4319	0·5438	0·6166
Error	72	0·0687	0·2032	0·1219	0·0729	0·2427	0·1494	0·0981
Residual	74	0·0685	0·1992	0·1235	0·0723	0·2365	0·1508	0·1003
Sq. Rt. Resid.		0·2617	0·4463	0·3514	0·2689	0·4863	0·3883	0·3167
$\times t_{DF}$ p 0·05		0·5129	0·8747	0·6887	0·5270	0·9531	0·7611	0·6207
Antilog		3·258	7·494	4·883	3·365	8·976	5·769	4·176

	Calanus finmarchicus Mean Squares					
	M		F		Stage V	
	DF		DF		DF	
Nets	2	0·0060	2	0·0758	2	0·0328
Stations	17	0·1794	31	0·1693	14	0·1807
Error	34	0·0540	62	0·0455	28	0·0408
Residual	36	0·0513	64	0·0465	30	0·0403
Sq. Rt. Resid.		0·2265		0·2156		0·2007
(a) $\times t_{DF}$ p 0·05		0·4439		0·4226		0·3934
(b) $\times t_{DF}$ p 0·1		0·3726		0·3546		0·3301
Antilog (a)		2·779		2·646		2·474
Antilog (b)		2·358		2·262		2·138

Mean confidence limits for "all animals":— 24 %—414·8 %
Mean confidence limits for *Calanus*:— at t . p 0·05:— 38 %—263·3 %
at t . p 0·1:— 44·4 %—225·3 %

cruises. He has kindly allowed me to use results from cruises when three Hensen egg-nets were used at each station.

The numbers of each sex and copepodite stage of each species in each haul were transformed by logarithms (Winsor and Clarke, 1940) and were subjected to an analysis of variance. This was carried out in order to make the distribution normal. There is usually a regressions of the variance on the mean in the distributions of plankton organisms. The purpose of the logarithmic transformation is to remove this regression, i.e., to make the variance and the mean independent of one

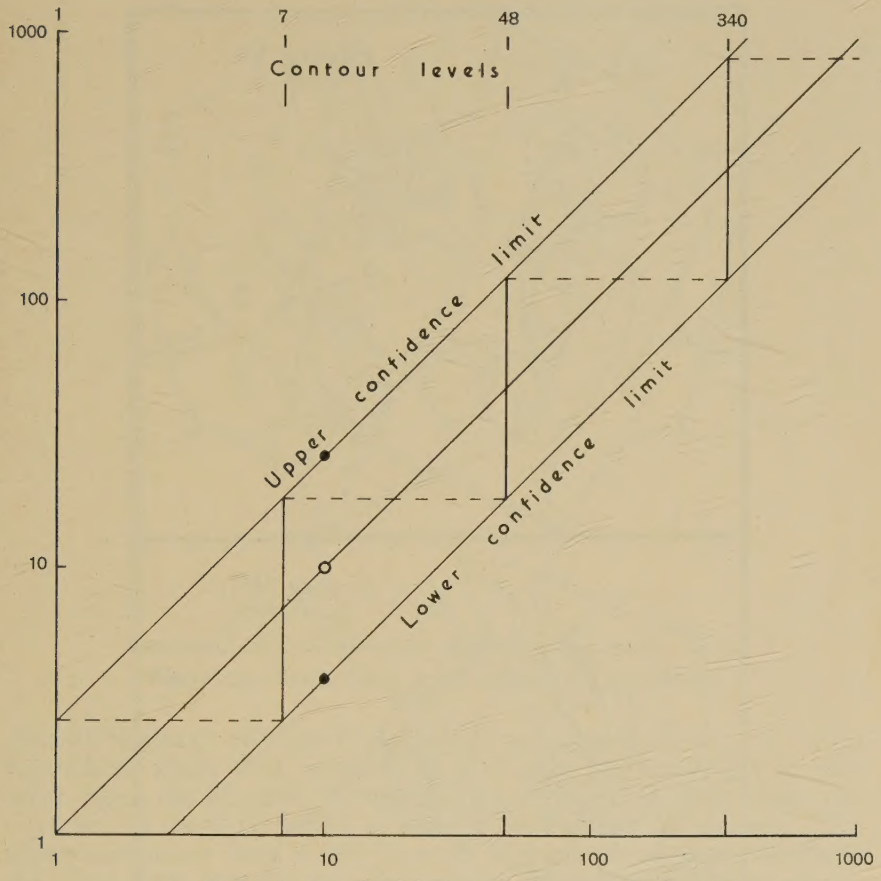


Figure 1. Graphical derivation of contour levels.

another. After the transformation had been carried out, there remained no regression between the two parameters.

Analyses of variance were carried out on each copepodite stage and each sex of each animal species, between the stations of the cruise and between the three nets hauled at each station. The Main Effect "Nets" was never significant and was always pooled with the error to form a Residual. The standard deviation of an observation at a station was obtained by taking the square root of the Residual variance. The standard deviation was multiplied by $t_{DF,\ p\,0{\cdot}05}$, and the product was antilogged to give the confidence limits to be attached to one observation. The upper limit for "all animals" is 4·148 (or 414·8 %) and the lower limit was $\frac{1}{4 \cdot 148}$ or 24 %; for *Calanus* only, these limits were 263·3 % and 38 %.

Figure 1 shows how contour intervals may be determined graphically, using these confidence limits. The numbers along the ordinate and

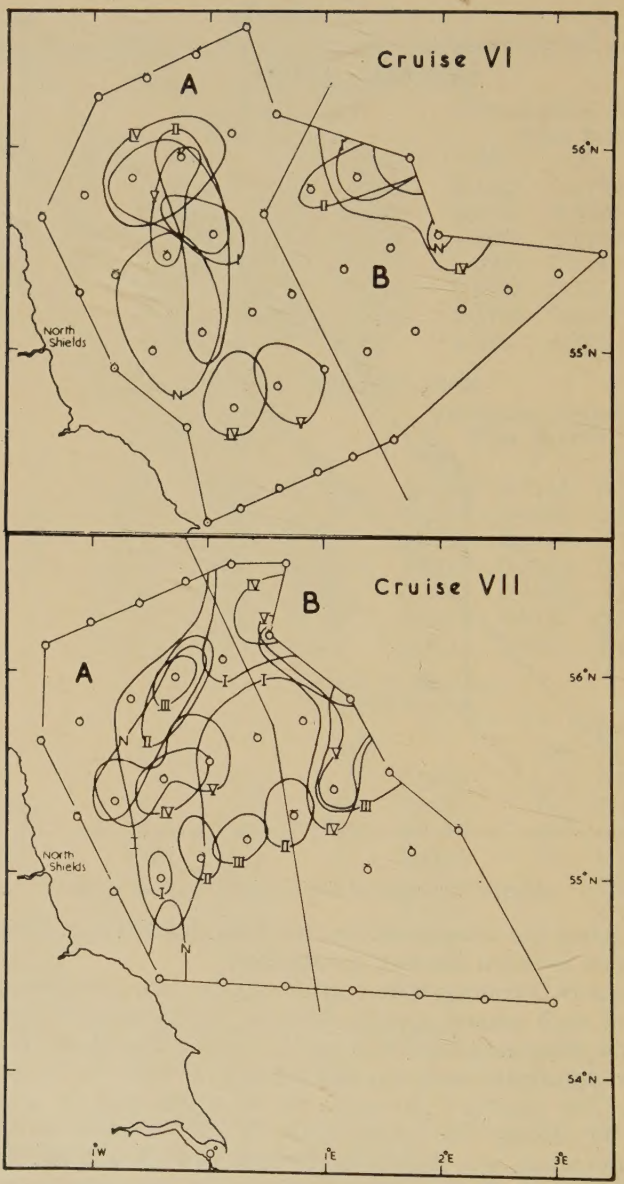


Figure 2(a). Cruises VI and VII. Patch groups of *Calanus* stages off the north-east coast in 1949. Each outline represents the highest contour level for a given copepodite stage: the number of the stage is inset in the outline (in Roman numerals). Stations are represented as circles.
The patch groups are named "A" and "B".

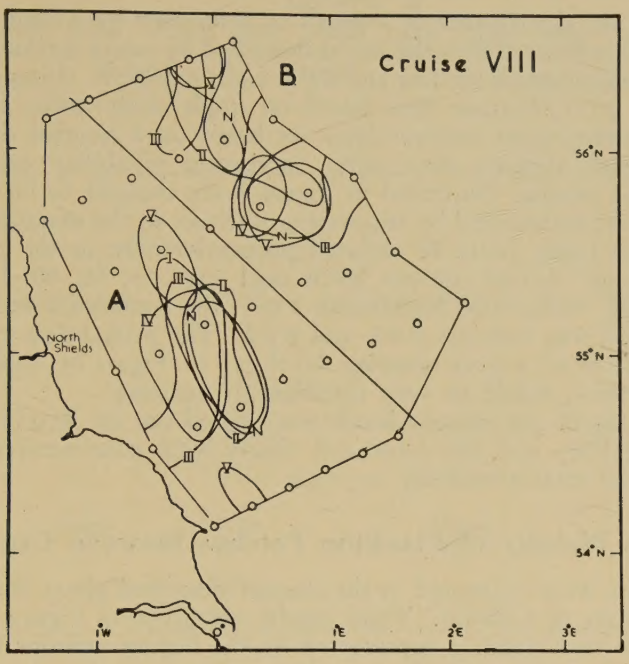


Figure 2(b). Cruise VIII. Patch groups as in Figure 2(a).

abscissa represent numbers of an animal species underneath 1 m^2. on a logarithmic scale; thus, numbers on both axes are equivalent to each other along the bisector. To use the graph, take a number along this bisector, e.g., $n = 10$ which is marked on Figure 1 by a circle. The upper confidence limit is 263 % or at 26·3 on the ordinate; similarly the lower limit is at 3·8 on the ordinate. These points are put on the graph on the ordinate, where $n = 10$ on the abscissa. Lines parallel to the bisector are then drawn through the points; the lines made in this way represent confidence limits for any number on the bisector, read off in a vertical direction. For $n = 7$, it is unlikely that any sample should derive from a population value outside the range 2·6—18. If one contour level is drawn at $n = 7$, the next one above should be drawn so that the lower confidence limit is at $n = 18$, that is, the contour level should be at $n = 48$. On the graph this is done by reading along the horizontal line at $n = 18$ (on the ordinate) from the upper confidence-limit line to the lower confidence-limit line. Thus the contour levels can be read off along the abscissa from the vertical lines between the confidence-limit lines. For numbers of *Calanus* male, female, stage V, in this example the contour levels are 1, 7, 48, and 340 underneath 1 m^2.

These contour levels are very wide indeed. They are set at p 0·05; at a higher level of probability, the confidence-limit lines would be closer together. If one considers the contour level in relation to one observation, p 0·05 is the appropriate probability. If, however, one

considers the significance of a patch as delineated by a contour line, it must be remembered that the line is described by many stations, e.g., one or two stations inside the line and six or eight outside it. Using confidence limits at p 0·1, contour lines based on single observations are unreliable; however, most contour lines are based on a number of observations, which support each other, increasing reliability considerably. Nearly all patches illustrated in Figure 2 are thought to be quite reliable; all are surrounded by supporting stations, so the magnitude of the confidence limits could be reduced proportionately to the number of observations. Actual contour levels used were 15, 30, 60, 120/m^3. or 1000, 2000, 4000, 8000 underneath 1 m^2.; the confidence limit for one observation was between p 0·1 and p 0·2. The probability of the confidence limit of a peak contour level (as in Figure 2), supported by many stations, would be very considerably reduced.

Drawing of the contour levels was carried out by Wollaston's method (1926) and the contoured charts were planimetered, to give estimates of total numbers.

The Identity of Plankton Patches between Cruises.

Patches were contoured in the manner described above for all copepodite stages of *Calanus*. These results are given in Figure 2, (a) and (b), where each patch is represented by the highest contour level used. This may include within its boundary only one station, but there are nearly always two or more stations supporting it in four or perhaps eight directions. It is seen that patches of each *Calanus* copepodite stage are in two recognizable groups A and B, maintaining their separation through the first three cruises. The area of low density separating the groups is fairly well maintained. Each group includes the same copepodite stages.

Table 2. Dates of the five cruises carried out off the north-east coast of England in 1949.

Cruise VI	10.—19. April 1949
VII	22.—30. April 1949
VIII	9.—18. May 1949
IX	23. May—1. June 1949
X	8.—14. June 1949

Turning to the problem of finding the identity of patch groups between cruises, it is clear that within this quite small region and comparatively short time interval between cruises, any patch group could move in any direction, particularly if the Firth of Forth swirl extends into the area.

It was hoped that size distributions might be helpful, especially as Bogorov (1934) found that the sizes of copepodite stages I—III were unimodal. On the other hand the sizes of copepodites in stages IV—VI would include variations due to sex differences and perhaps to the

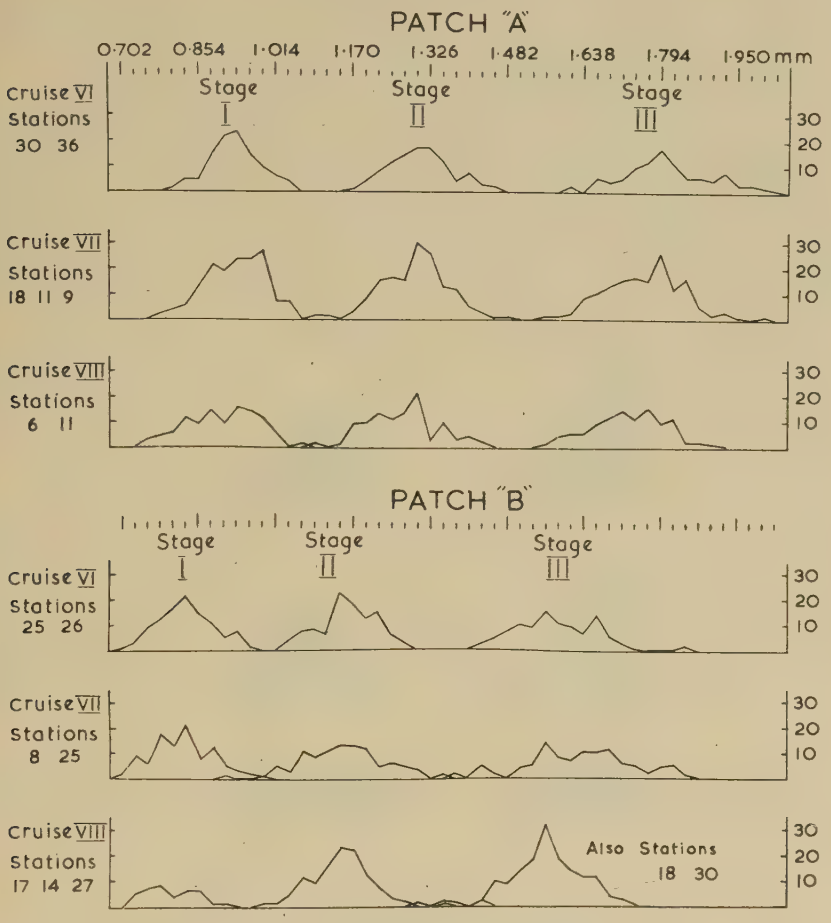


Figure 3. Frequency distributions of *Calanus* copepodite stages I—III from patch groups "A" and "B", during Cruises VI—VIII.

possible division between *Calanus finmarchicus* and *Calanus "helgolandicus"*. A number of specimens of stages I—III was measured from stations clearly within each group. Figure 3 shows the results; the frequency distributions were polymodal and were arranged along a scale of length, so that each set of three stages can be compared by noting its position on the scale relative to the set above or below. It is immediately clear that the copepodite stages I—III in the "A" group of patches are consistently larger than those in the "B" group. Within each group ("A" or "B") the sizes of the three stages remain consistently the same for the three cruises. Thus it is reasonable to assume that the "A" group in Cruises VI—VIII are in fact the same group; this might also be said of the "B" group, but this is not completely sampled. A consequence of this lucky observation is that the "A" group is said to flow in from the north-east and out to the south past Whitby; this is

in accord with the hydrographic evidence. In Cruise IX the "A" group is no longer present, having presumably drifted out to the south.

A useful consequence of the identity of the "A" group between cruises is that it is possible to make an age distribution of the copepodites of *Calanus*. If it is assumed that *Calanus* moult, passing from one stage to the next, in about fourteen days, this would give a moult between each cruise for which the time intervals were (VI—VII) 13 days, and (VII—VIII) 18 days. This is not unreasonable, for R u u d (1929), F i s h (1936), and R e e s (1949) suggest that the total develop-

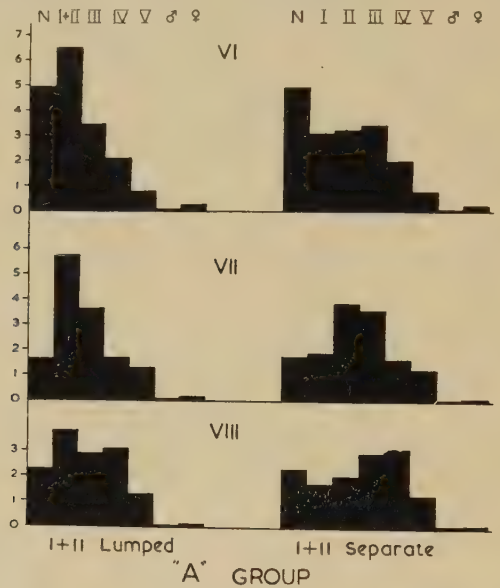


Figure 4. Age distribution of *Calanus finmarchicus* copepodite stages in the "A" patch group. Each column in the histogram represents an estimated number $\times 6{\cdot}4 \times 10^{13}$.

ment time is from 70—90 days. Figure 4 shows the age distribution that can be made from the numbers of successive copepodite stages in the "A" group. It may be observed that there is a resemblance between the distributions of the three cruises. The relative proportions of *Nauplii*, copepodite stage I and stage II to other stages in Cruise VI are similar to those of stage II and III to other stages in Cruise VII, and again to those of stage III and IV in Cruise VIII. There are two other features about these distributions, namely, the sharp decline in numbers of recruits as time goes on (related almost certainly to an equally sharp decline in the numbers of plants) and the much steeper mortality apparent in the older stages. The latter might be due to herring and other predators.

We have thus obtained information on two of the balancing factors in the *Calanus*—herring relation; the next method deals with the numbers of the herring.

The Use of the Echo-Sounder in the Study of the *Calanus*—Herring Relation.

The estimation of abundance of pelagic fish over such a wide area is not possible from commercial catches, because the fishermen use drift-nets, from which catches are very irregular, and the fleet does not cover the area well. To overcome this, on reconnaissance cruises in 1948, a method of echo-survey was devised (Cushing, 1952). The echo-traces were not specifically identified as herring, because variations in the shapes and sizes of echo-trace can be caused by shoaling behaviour only; nevertheless, in this area and season, there is a high probability of herring being the cause of an echo-trace. Strictly, however, the estimates here are not necessarily of herring, but certainly of pelagic fish. There was no difference between the number of shoals observed by night and by day; thus it is unlikely that any diurnal change of behaviour was taking place.

The results were charted as numbers of echo-units between plankton stations; these were contoured and planimetered to give indices of the abundance of pelagic fish. The results in relation to the *Calanus* patches are shown in Figures 5 and 6. In Cruises VI and VII, there is no relation between *Calanus* and pelagic fish (Figure 5) but in Cruises VIII—X, there is sharp and vivid aggregation (Figure 6). As aggregation proceeds, the numbers of pelagic fish become greater and then in Cruise X they die away again.

Table 3. Correlation coefficients between echo-units and zooplankton densities, Cruises VI-X, "Sir Lancelot", 1949.

Cruise	VI	VII	VIIII	IX	X
Calanus finmarchicus					
Stage I	0·1	—0·3	0·3	0·2	0·3
Stage II	0·2	—0·3	0·2	0·3	0·3
Stage III	0·3	—0·2	0·5**	0·2	0·4
Stage IV	—0·4*	—0·2	0·2	0·3	0·7**
Stage V	—0·3	—0·3	0·4*	0·3	0·1
Stages IV and V	—	—	0·3	0·2	0·5*
Paracalanus parvus					
Female	—0·1	—0·1	0·2	—0·2	0·1
Juvenile	—0·1	—0·2	0·2	—0·1	0·1
Pseudocalanus elongatus					
Male	0·1	0·0	0·0	—0·1	0·0
Female	0·2	—0·2	—0·1	—0·1	—0·3
Juvenile	—0·2	—0·3	0·1	—0·0	—0·1
Temora longicornis	0·5**	0·3	—0·0	—0·1	0·2
Evadne Nordmanni	—	—	—	—	—0·2

*Significant at p 0·05 **Significant at p 0·01

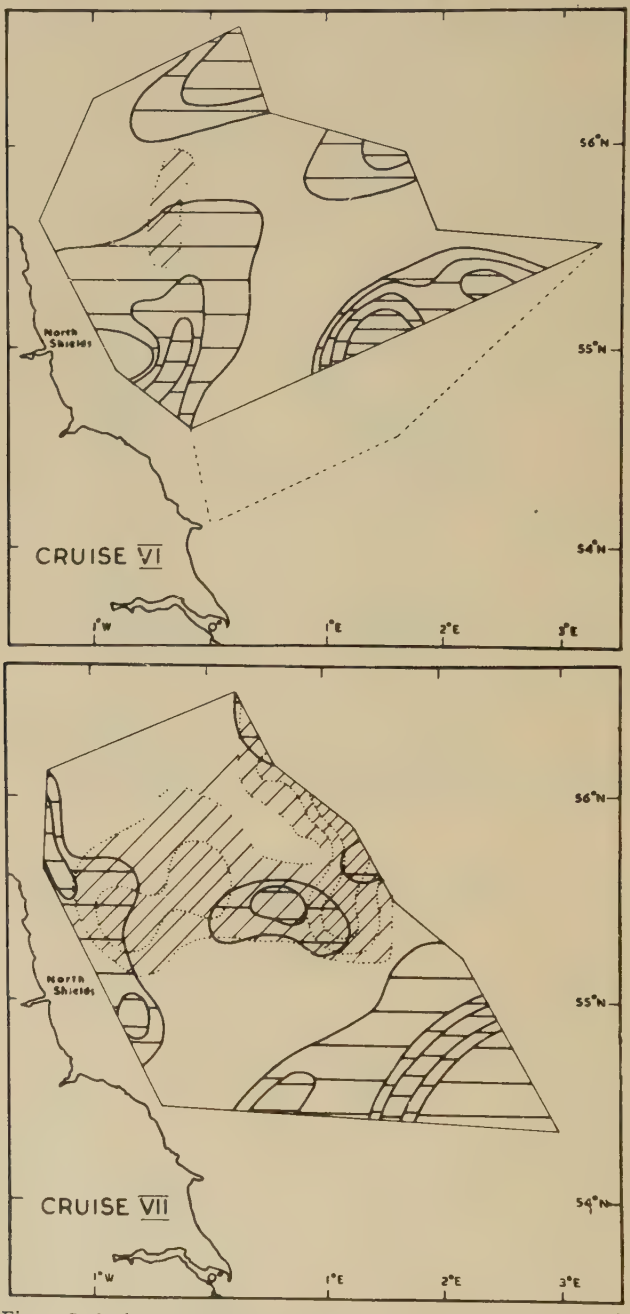


Figure 5. Relation between *Calanus* and echo-units. The *Calanus* distributions are represented with the contour levels surrounded by dotted lines; the echo-unit distributions are represented with the contour levels surrounded by full lines.

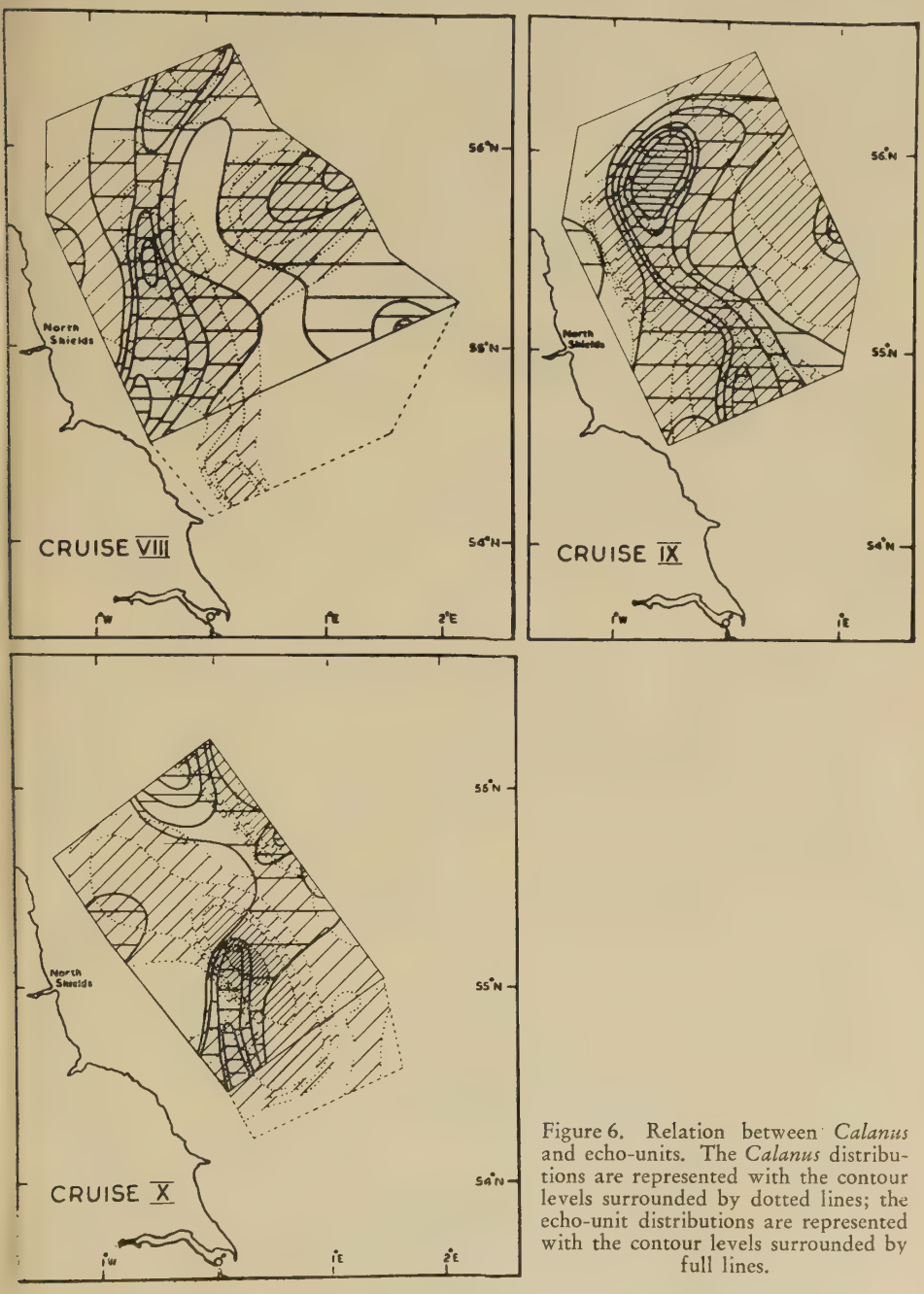


Figure 6. Relation between *Calanus* and echo-units. The *Calanus* distributions are represented with the contour levels surrounded by dotted lines; the echo-unit distributions are represented with the contour levels surrounded by full lines.

Table 3 shows the same effect in another way. Numbers of *Calanus*/m^3. at plankton stations were correlated with numbers of echo-units between plankton stations. Correlation coefficients are shown for all the copepodite stages of *Calanus* and the more abundant "other copepods" for all five cruises. The correlation coefficient is being used as a measure of the aggregation between the distributions of *Calanus* and pelagic fish; for this purpose the sign of the coefficient and its magnitude are more important than whether it is significant. During Cruise VIII and later cruises, there are only positive correlations and most correlations with "other copepods" are inverse. This is taken to mean that aggregation has taken place on to the *Calanus* patches. Again, the higher coefficients are found with the stages IV and V. A third interesting point is that during Cruises VIII—X, the coefficient for stage V declines markedly, whilst that for stage IV increases equally sharply. This cannot be related to size or numbers of *Calanus* stages, and it is tempting to ascribe it to grazing.

The *Calanus*—herring relation consists of three balancing processes, the rate of aggregation of the herring on to the *Calanus* patch, the rate of reproduction of the *Calanus* population, and the rate of consumption of *Calanus* by the herring (and the subsequent disengagement of the herring).

Aggregation by Drifters.

It was quickly realized that there was an analogy between the *Calanus*—herring relation and that between the herring and the searching drifters. Drifters aggregate in patches on to patches of herring, exploit the patches, and then disengage. The analogy must not be pressed too far. One might assume that herring aggregate in movements that are random in direction, but slower in speed within *Calanus* patches than outside them. The movements of drifters are not random in direction and are governed to a high degree by the spread of the latest information. However, drifters do aggregate on to herring patches, they do exploit them, and they do disengage from them, to aggregate elsewhere.

Catches of herring are recorded as quantity from a given position on a particular night. These positions are not very accurate and are expressed as catches in rectangles of approximately 10×6 miles for East Anglia and 10×10 miles for North Shields. The difference in area between East Anglia and North Shields rectangles will make a slight change in the slope of the regression of boats on catch at North Shields but will have no effect on the sign of the regression, positive or negative. The catch is expressed as the mean catch per rectangle per night in crans; this is a rough measure of the abundance of fish. The abundance of drifters is expressed as numbers of boats per rectangle per night. The relation between the abundance of drifters and the abundance of fish is shown in Figure 7. Each graph in this figure shows two regressions, (a) a linear regression of the number of boats per rectangle upon the mean catch per rectangle and (b) a curvilinear regression of the mean catch

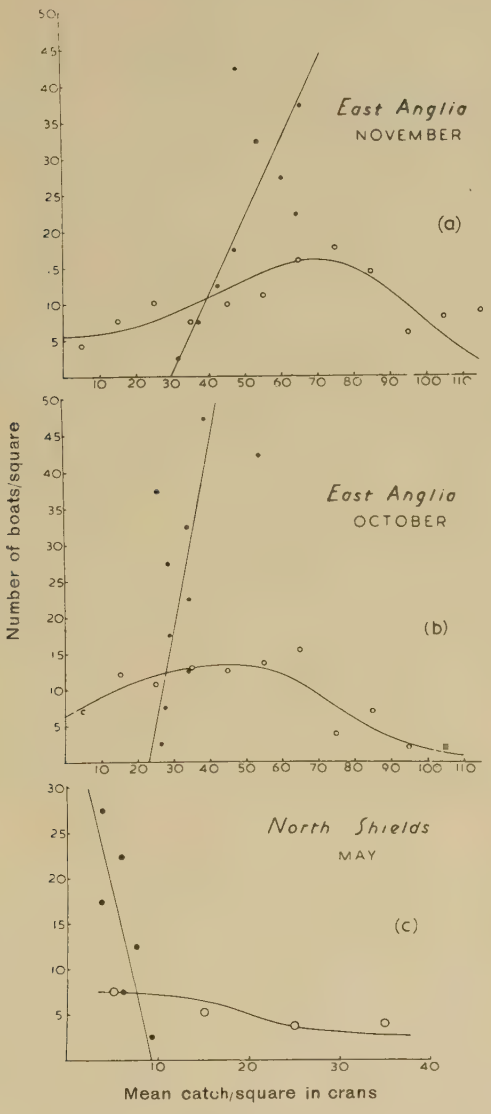


Figure 7. Relation between the number of boats per 10 mile square and mean catch per 10 mile square.
The linear relation shows the dependence of the number of boats per square upon the mean catch per square.
The curvilinear relation shows the dependence of the mean catch per square upon the number of boats per square.

per rectangle upon the number of boats per rectangle. The first regression shows the condition of aggregation and the second shows an estimate of the abundance of fish.

It will be seen that there are three conditions of aggregation according to three levels of abundance. Off East Anglia in November, the greater the number of boats, the greater the mean catch. This means that the aggregative process is dominant, that most efficient searching is obtained with the largest fleet; thus the shoals must be very large or must be moving very quickly. Off North Shields in May, the aggregative process is no longer dominant, for the greater the number of boats, the smaller the catch. This means that the exploiting process is dominant; it appears that searching plays a minor part. In this fishery the shoals must be very small. The East Anglian fishery in October shows the intermediate case, in which the aggregative process balances the exploiting process. The three conditions of aggregation are related to abundance as follows:— (a) off East Anglia in November, the mean catch is approximately 52 crans/night/boat; (b) off East Anglia in October, the mean catch is approximately 36 crans/night/boat; (c) off North Shields in May, the mean catch is approximately 6 crans/night/boat. It must be pointed out that exploitation in this context means a decrease in the mean catch, which may be due to fishing, to interference with the shoals by the drift-nets, or to emigration by the fish; the method will not distinguish these effects.

The conclusion is that the efficiency of searching depends upon the relation between numbers of drifters and numbers of fish; again the disengagement of drifters from a fish patch depends upon the rates of change of these numbers relative to each other. This is the extent to which the analogy with the *Calanus*—herring relation is fruitful.

Diatom Division Rates.

Phytoplankton reproduction is usually estimated indirectly (R i l e y *et al.*, 1949; N i e l s e n, 1951). It is possible to estimate the number of divisions that took place between cruises for diatom species. Diatom species were measured from samples from the "A" group on each cruise; the decrease in cell size that takes place as the diatoms divide was then estimated. If the width of the cell wall of a diatom species is known, it is possible to make an estimate of the number of divisions between cruises that have taken place, by dividing the cell-size decrease by the cell-wall width (see Figure 8). Figure 9 shows an electron microphotograph of *Chaetoceras decipiens* (× 4050). It is obviously possible to use several measurements; in fact, the distance across the cell wall, radially, was used. Two types of diatom were found, (a) those that show a decrease in cell-wall width with decrease in cell size (*Thalassiosira, Skeletonema*), and (b) those that show no such relation (*Chaetoceras*).

Diatoms from the Fine net samples from the "A" patch were measured and the polymodal distributions were split by probit analysis. The populations from Cruises VI and VII were compared and cell-size decreases estimated. From the cell-size decrease and the cell-wall size, it

was possible to find the number of divisions that had taken place between cruises. An example is given in Table 4.

Table 4. Decrease in cell size and the number of divisions between Cruise VI and VII for *Chaetoceras compressus*.

	Cruise VI		Cruise VII		Mean Decrease in μ	Cell-Wall Width	Divisions
	$\bar{x}$	S. D.	$\bar{x}$	S. D.			
Chaetoceras	49·0	7·5	40·0	4·0	2·530	0·17	14·8824
compressus	65·0	7·0	48·5	4·5			
	80·5	13·0	71·5	7·0			

An estimate of the natural mortality of diatoms was made by counting the number of complete and empty frustules; it was assumed that they sank 10 m. per day (see Apstein, 1896, and Gross and Zeuthen, 1948). It was then assumed that any other mortality was due to herbivore grazing.

We have estimates of numbers, division rate, and rate of natural mortality for a number of diatom species. It is possible, using these figures, to estimate the total plant production between cruises. It was assumed that any loss in numbers between cruises not accounted for by natural mortality is due to herbivore grazing. My colleague, John Gulland, has developed for me the following methods, using this form of equation: —

$$\frac{dP}{dt} = -K.a_o.P + (R - M)P$$

$$P_1 = P_0.e^{(R - M - K.a_o)t}$$

$$K.a_o = \frac{(R - M)t - \log_e \frac{P_1}{P_0}}{t}$$

Total production is

$$\frac{P_0 \cdot R}{R - M - K.a_o}\left[e^{(R - M - K.a_o)t} - 1\right]$$

Total natural mortality is

$$\frac{P_0 \cdot M}{R - M - K.a_o}\left[e^{(R - M - K.a_o)t} - 1\right]$$

Number of plants grazed is

$$\frac{P_0 \cdot K.a_o}{R - M - K.a_o}\left[e^{(R - M - K.a_o)t} - 1\right]$$

P is the number of diatom species in a cruise.
P_0 is the number of a diatom species in Cruise VI.
P_1 is the number of a diatom species in Cruise VII.
$K.a_o$ is the coefficient of herbivore grazing.
M is the coefficient of natural mortality.
t is the time in days between the two cruises.

These formulations are analogous to those used by Ricker (1946) and Allen (1950).

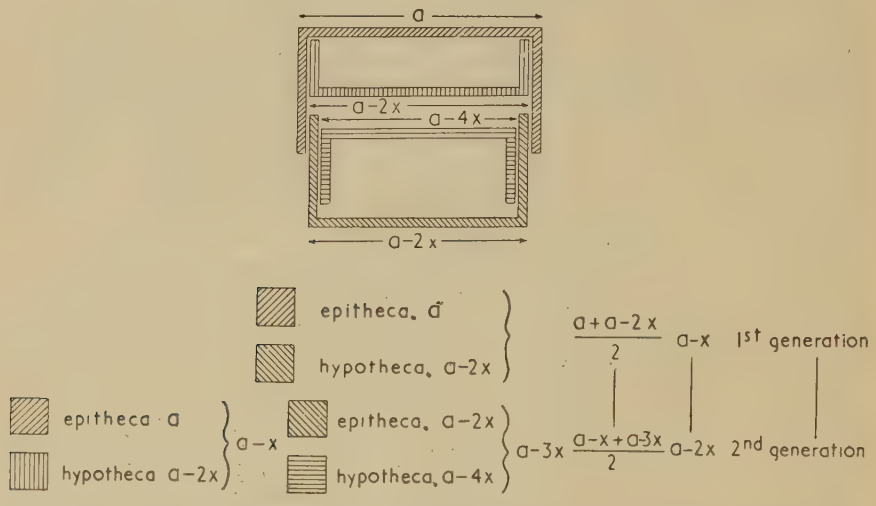
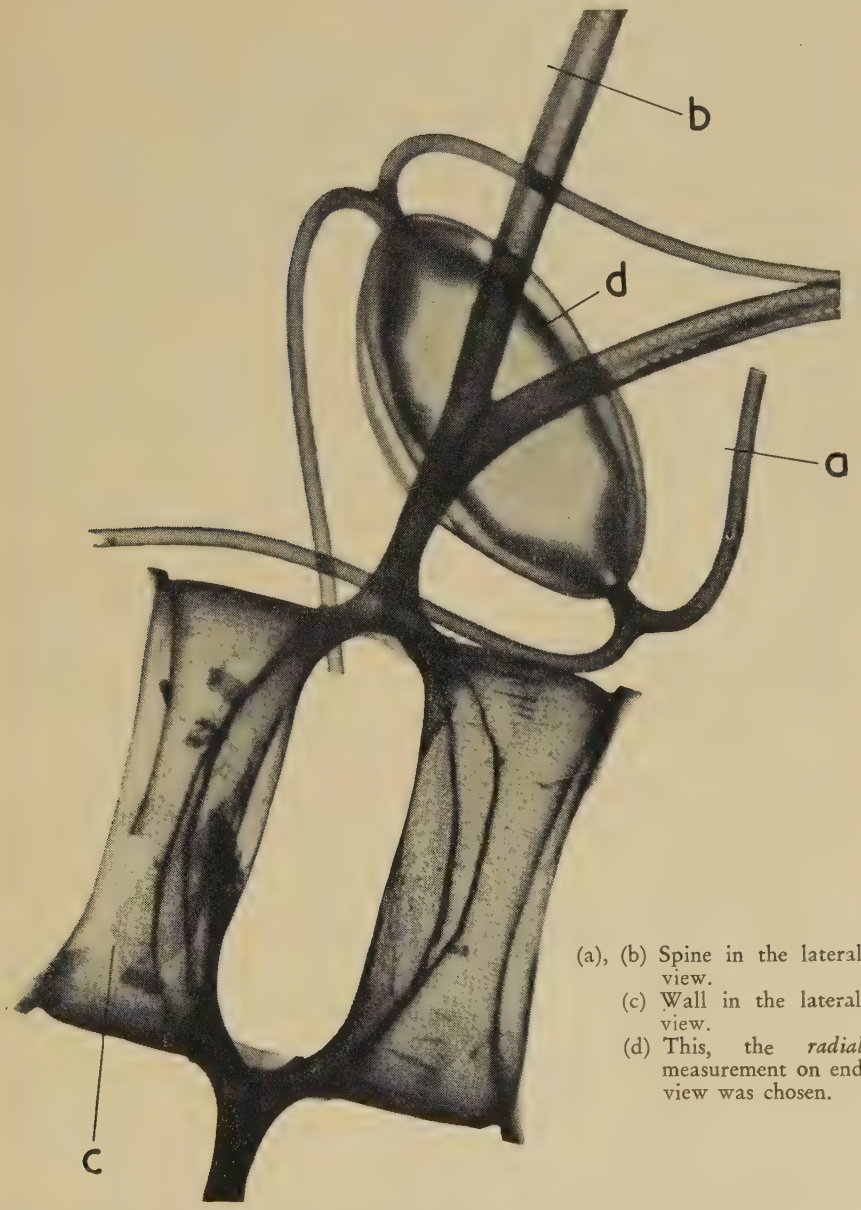


Figure 8. The decrease of diatom cell width at division. As any measurement in transapical width must be the mean of the epithecal and hypothecal widths, the difference in mean width between each division is one cell-wall width, x. The measurement of the first generation cell is $\frac{a+a-2x}{2}$ or $a-x$; the measurement of the second generation cell is $\frac{a-x+a-3x}{2}$ or $a-2x$.

The figures, so derived, were used in this way. An estimate was made of the amount of food eaten by each group of herbivores. The numbers of animals, by species and, for *Calanus*, by copepodite stages, were multiplied by the cubes of their lengths, in order to obtain a measure of the grazing capacity of the different herbivores; grazing capacity was assumed to be proportional to the volumes of herbivores. The numbers grazed of each diatom species were multiplied by their volumes. Thus it was possible to sum the total volume of grazed plant production. This grazed plant production was then split in the proportions of the herbivore grazing capacities. It was assumed that grazing was equally intense over the period between cruises and so it was possible to make estimates of the quantity of plant material taken in by each copepodite stage of *Calanus* per day:—

Stage I	II	III	IV	V	Adults	
$6{\cdot}56 \times 10^{-2}$	$1{\cdot}54 \times 10^{-1}$	$5{\cdot}35 \times 10^{-1}$	$1{\cdot}46 \times 10^{-1}$	2·97	5·68	mm.³ plant material/ day

There is no reason why this method should not be extended to diatom species. Thus the elements of H a r d y ' s famous picture of the herring food chain may be estimated quantitatively.



(a), (b) Spine in the lateral view.
(c) Wall in the lateral view.
(d) This, the *radial* measurement on end view was chosen.

Figure 9. Electron photomicrograph of *Chaetoceras decipiens*. This shows the possible measurement that one might take to obtain the cell-wall thickness.
(Phillips microscope, ×4050, 60 kv., taken for me by Mr. Ripley of the Biophysics Sub-Department, Department of Botany, Leeds University.)
Professor Braarud and Mr. Grøntved have pointed out to me that the valve view is probably one of a resting spore of *Chaetoceras cinctus*.

Discussion.

Four methods have been introduced in the study of plankton populations. The separation of contour levels allows one to make adequate estimates of the numbers of these populations in the sea. The measurement of the smaller copepodite stages has allowed me to identify some of these populations from cruise to cruise. The use of the echo-sounder to survey pelagic fish populations makes it possible to make estimates of the numbers of herring (and other pelagic fish) associated with these pelagic fish populations. Studies of cell sizes have led to estimates of diatom division rates. The four methods are all connected to one problem and this is the production cycle in the sea.

Each method is concerned with the estimation of numbers of fish or plankton population. Up till the present it has been more usual to find the energy relations of the production cycle; this is because it has been impossible to estimate diatom division rates. There is a loss of energy as it passes up the food chain and the only connexion between parts of the chain is the loss of "efficiency" between them. The crux of the dynamic method as developed in this paper is that the parts of the food chain are assumed to depend upon each other by the parameters of their own systems. Thus, the *Calanus* population may be described in terms of its reproduction rate and its death rates; its reproduction rate is dependent on the production of the plants and its death rate is partly dependent on the aggregation of the herring.

The simplest production cycle or dynamic cycle is that which has been dealt with in this paper. It may be described symbolically in the following terms:—

$$\frac{dP}{dt} = (R_p - G_h - M_p)\,P$$

$$\frac{dH}{dt} = (R_h - G_f - M_h)\,H$$

$$\frac{dF}{dt} = -(G_d + M_f)\,F + (I_f - E_f)\,F$$

$$\frac{dD}{dt} = (I_d - E_d)$$

R_p reproduction of a plant species.
R_h reproduction of a herbivore sp.
I_f immigration of a fish species.
E_f emigration of a fish species.
I_d immigration of drifters.
E_d emigration of drifters.

M_p "natural" mortality of a plant sp.
M_h "natural" mortality of a herbivore sp.
M_f "natural" mortality of a fish sp.
G_h grazing mortality of a plant sp.
G_f grazing mortality of a herbivore sp.
G_d grazing mortality of a fish sp.

The equations for fish and drifters differ from those for plants and herbivores in that the numbers of fish and drifters are also dependent upon the numbers of fish and drifters elsewhere. The lines between the trophic levels indicate dependences, but no attempt is made to shed light on the nature of these dependences.

At each trophic level these equations are worked out for each species; the grazing coefficients are worked out as total herbivore effect or total fish effect. The importance of this arrangement is that there is a two-way dependence between each level. It is perfectly possible to deal with each level separately, but understanding will only come by analysing the whole system. The practical point is that if we need to understand aggregation in a feeding pelagic fishery, this type of method is essential.

A distinction has long been made between actual and potential production. Measures of potential production in the sea are those like the winter phosphorus maximum or total phosphorus. Actual production in the sea is measured by estimating the standing crop of plants and its reproductive rate or "production coefficient" over a period of a year. The estimate of potential production differs from that of actual production in two ways:—

(a) Between trophic levels in the food chain, there is a loss of production, as material produced or energy used.

(b) As phosphorus may be put through the productive cycle more than once in a year, an actual production of plants may be greater than the potential.

The use of plant material produced has been traced part of the way up the food chain by using a kinetic approach. F l e m i n g (1939) was not interested in diatoms as individuals, but in their ability to fix carbon, nitrogen, and phosphorus; similarly R i l e y *et al.* (1949) have used a system in which plant production is estimated from the photosynthetic rate and the respiration rate. This gives plausible results, but the systems at each trophic level are not necessarily connected; there is increasing loss of energy, the further the food chain is extended from the plants. The dynamic method assumes (and quite reasonably) that the systems at each trophic level are connected with each other by their own parameters.

This is an extension of the idea of actual production. Theoretically, it should be possible to extend the survey of this actual production to the yield of fish in a feeding fishery or to the amount of growth put on by fish in a year. The latter is obviously inaccessible because all fish populations cannot be sampled in this way all the time. The former, the yield of fish, however, is only that part of the actual production that men like to eat. This is what we are really interested in and we may call this part of the production the useful production. This is affected in two ways by variations in actual production:—

(a) The increment of fish flesh for a period of time will depend upon the quantity of food produced.

(b) The availability of fish for catching during a similar period of time will depend upon the distribution of the fish and its food in time and in space.

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La Fonction Hypophyso-Thyroïdienne des Poissons dans ses Rapports avec leur Morphologie et leur Comportement.[1])

Par

M. Fontaine.

LES océanographes biologistes ont été assez souvent préoccupés des différences morphologiques ou éthologiques existant entre des races ou des populations de poisson pour que maintes études aient été déjà consacrées aux facteurs susceptibles de promouvoir de telles différences. Mais les plus nombreuses sont celles consacrées aux facteurs externes. Beaucoup plus rares sont celles relatives aux facteurs internes qui interviennent cependant en corrélation avec les facteurs externes.

Chez les vertébrés supérieurs, le retentissement des variations d'activité de certaines glandes endocrines sur divers caractères morphologiques et sur le comportement n'est plus à démontrer. L'action de l'hormone thyroïdienne notamment et du stimulant de la glande thyroïde d'origine hypophysaire (l'hormone thyréotrope) a été, à maintes reprises, soulignée.

Toutefois l'extension de ces faits à la classe des poissons a rencontré certaines objections dont la principale est la suivante: chez les mammifères, l'hormone thyroïdienne exerce sur le métabolisme respiratoire une action accélératrice absolument classique. Or, chez les poissons, la plupart des auteurs qui ont tenté de mettre en évidence cette action ont échoué.

En 1935, Drexler et Issekutz n'ont pas trouvé de changement dans le métabolisme respiratoire du *Girardinus guppyi* traité par la thyroxine, celle-ci étant administrée en bain à la concentration de 1/500,000. En 1937, Root et Etkin, expérimentant sur l'*Opsanus tau*, constatent que des injections de thyroxine même massives, n'exercent aucun effet notable sur le métabolisme respiratoire de ce poisson.

[1]) Soulignons que la fonction hypophysaire n'est pas ici étudiée dans son ensemble et qu'il y est fait simplement allusion pour sa sécrétion thyréostimulante.

Cependant, sur les mêmes individus, des injections de 2—4 dinitrophénol entraînent une élévation de près de 100 % du métabolisme, ce qui montre qu'ils sont capables de répondre à un agent efficace.

En 1940, Etkin, Root, et Mofshin n'ont pu trouver de changement du métabolisme respiratoire du poisson rouge en le nourrissant de poudre de thyroïde desséchée pendant une durée allant jusqu'à 38 jours. En 1942, Hasler et Meyer ne constatent également aucun effet de la thyroxine sur les échanges respiratoires du cyprin doré, mais une action accélératrice de l'hypophyse de carpe. En 1943, Smith et Everett constatent que ni la thyroxine, ni la poudre de thyroïde n'exercent d'action sur l'intensité respiratoire du *Lebistes reticulatus*. Et en 1945, Punt et Jongbloed constatent que la thyroxine ajoutée à l'eau n'a aucune influence sur le métabolisme respiratoire du *Rhodeus amarus* L. Ils émettent alors l'hypothèse que cette inactivité pourrait être attribuée au fait que la thyroxine ne traverse pas l'épithélium branchial. Mais certaines expériences des auteurs précédemment cités ont démontré que même injecté, ce corps est sans action.

Seuls, plus récemment Smith et Matthews, ayant préparé des extraits de glande thyroïde des poissons perroquets des Bermudes ont constaté que de tels extraits injectés à des *Bathystoma* sont capables d'élever de façon très importante (75 %) le métabolisme respiratoire de ces poissons pourvu que ceux-ci ne soient pas de trop petite taille. Il faut remarquer que les auteurs précédents avaient tous utilisé de la thyroxine ou des poudres thyroïdiennes de mammifères alors que Smith et Matthews emploient une poudre de thyroïde de poisson. Ainsi apparaît-il possible que, au moins dans certaines conditions, l'hormone thyroïdienne des poissons agisse sur leur métabolisme respiratoire, comme le fait l'hormone thyroïdienne des mammifères sur le métabolisme respiratoire des mammifères. La découverte récente dans le sang de mammifères de la triiodothyronine, plus active sur le métabolisme que la thyroxine, pose d'ailleurs le problème de la pluralité des hormones thyroïdiennes à efficacités diverses même chez les mammifères. Il n'est donc pas très étonnant que, chez les poissons, la thyroxine n'exerce pas d'action notable sur le métabolisme respiratoire.

On a cherché si les antithyroïdiens étaient susceptibles de diminuer l'intensité des échanges respiratoires des poissons. Matthews et Smith (1947) n'ont pas obtenu d'action de la thiourée administrée en injection, sur la consommation d'O_2 du *Fundulus*.

Cependant nous avons obtenu des chutes importantes de la consommation d'O_2 chez des civelles traitées par la phénylthiourée en bains à 1/10,000 (résultats inédits).

D'autre part, Franco Tinacci (1947) a observé chez des *Mustelus levis* nourris avec du thiouracile, du méthylthiouracile et de l'aminothiazol une baisse des mouvements respiratoires et une résistance accrue à l'asphyxie qui semblent favorables à l'hypothèse d'une diminution de la consommation d'O_2 consécutive à l'administration des antithyroïdiens.

Enfin tout récemment Z a k s et Z a m k o v a (1952) ont montré que les jeunes saumons et esturgeons immergés dans un bain de thiourée à 0·33 ‰ voient leur consommation d'O_2 diminuer sensiblement par rapport aux témoins. D'autre part les poissons traités sont beaucoup moins sensibles à la baisse de pression partielle de l'O_2 que les poissons gardés dans de l'eau pure. Tout se passe comme s'ils étaient capables de mieux utiliser l'oxygène aux basses tensions d'O_2. L'action de la thyroxine surajoutée au bain de thiourée semble supprimer *pro parte* la diminution du métabolisme respiratoire entraînée par celle-ci.

Donc si certains liens ont pu être mis en évidence chez les poissons entre l'activité thyroïdienne et le métabolisme respiratoire, ceux-ci semblent moins nets et beaucoup moins constants chez les poecilothermes que chez les homéothermes. Peut on admettre avec H a f f n e r que, chez les poecilothermes, la thyroïde intervient surtout dans la phase anoxybiotique du métabolisme? L'expérience de v o n E u l e r montrant que du muscle de grenouille traité par la thyroxine ne présente une augmentation nette de la consommation d'O_2 que sous de très faibles tensions d'O_2 (quand le pourcentage d'oxygène dans l'air atteint 10 %), les travaux de H a r m s montrant que la thyroxinisation facilite l'amphibiose des poissons viendraient à l'appui de cette hypothèse.

Quoiqu'il en soit, la thyroïde des poissons semble bien fonctionner dans ses grands traits comme la thyroïde des vertébrés supérieurs et notamment on a montré qu'elle concentre le radioiode (M a t t h e w s et S m i t h, 1947; C. L i n, T e h P i n g et E d w a r d D. G o l d b e r g, 1951; L e l o u p, 1951; F o n t a i n e, L e l o u p et O l i v e r e a u, 1952) et fabrique de l'iode lié organiquement et présentant les caractères de solubilité de l'iode thyroxinien. D'autre part, des expériences variées prouvent incontestablement que l'hormone thyroïdienne intervient sur diverses fonctions et métabolismes des poissons. Tout d'abord, on sait que chez les mammifères, l'administration de thyroxine ou poudre de thyroïde pendant une durée assez prolongée entraîne la mise au repos de la glande de l'animal (C o u r r i e r). Or, on observe le même effet chez les poissons (V i v i e n et G a i s e r, 1952; F o n t a i n e et W u r t z, 1952).

Les expériences de H a r m s (1929—1935) sur les Gobiidés, les observations histologiques de S k l o w e r (1928—1930), sur l'anguille, tendent à montrer que l'hormone thyroïdienne intervient pour déterminer la métamorphose, de même que chez les Batraciens. Toutefois, V i l t e r (1946) a mis en doute l'action de la thyroxine sur la métamorphose larvaire de l'anguille. Mais, d'une part, il n'a pas étudié l'action de la thyroxine sur la métamorphose larvaire proprement dite de l'anguille (la larve de l'anguille étant le leptocéphale), mais seulement sur le passage de l'état de civelle à l'état de petite anguille. D'autre part, V i l t e r a pris comme critère d'action de la thyroxine son influence sur la pigmentation cutanée et l'accroissement de la longueur de l'estomac. Or, il observe une action accélératrice très nette de la thyroxine sur la pigmentation cutanée quelle que soit la concentration et une action nette sur la longueur de l'estomac quand la thyroxine est administrée à doses

croissantes. Ce résultat cependant, le conduit à se demander si les phénomènes observés ne reflètent pas "plutôt les conséquences de l'augmentation pharmacodynamique du métabolisme général qu'une intervention métamorphogène proprement dite", car, écrit-il, il n'y a "aucune perturbation du développement normal telle que nous révèle la thyroxinisation des Batraciens". Mais c'est que, dans ce dernier cas, on fait agir l'hormone sur une larve avant la métamorphose tandis que dans le cas de la civelle, Vilter fait agir l'hormone sur un animal après sa métamorphose larvaire. Quand on fait agir la thyroxine sur la grenouille et non sur le têtard, on n'observe pas une nouvelle métamorphose!

Bien d'autres actions de l'hormone thyroïdienne sur la morphologie des poissons sont d'ailleurs incontestables.

Harms a montré que l'ingestion d'hormone thyroïdienne par des Gobiidés tropicaux entraînait un allongement des nageoires pectorales et un épaississement de la peau. La Roche (1951) a récemment observé le même phénomène chez des Salmonidés. Chez la truite même, l'hyperplasie ne se localise pas au derme, mais s'étend au tissu conjonctif des organes internes. Krockert (1936) chez *Lebistes reticulatus*, puis Grobstein et Bellamy (1939) chez *Platypoecilus*, obtiennent, en incorporant de la poudre de thyroïde au régime alimentaire, un allongement des nageoires et une exophtalmie marquée. Petit et Schachter (1941) avaient déjà signalé chez les civelles l'apparition d'exophtalmie sous l'influence de bains de thyroxine. Grobstein et Bellamy (1939) observent en outre, un développement plus rapide (accélération de l'apparition du gonopode) et une croissance plus lente. Buser et Bougis (1951) observent les mêmes phénomènes sur *Gambusia* (allongement des nageoires pectorales et exophtalmie) par l'immersion dans des bains de thyroxine. L'étude de la production de l'exophtalmie par l'hormone thyréotrope hypophysaire chez *Fundulus* a été faite d'une façon particulièrement poussée par Albert (1945).

Svärdson (1943) constate que chez *Lebistes*, les individus traités par la thyroxine atteignent leur maturité génitale plus tôt et à une taille moindre que les témoins, mais la même année Smith et Everett n'observent aucune action sur la croissance et la maturation sexuelle de cette même espèce par administration de thyroxine et de poudre de thyroïde. Cependant Hopper (1950) constate que de jeunes *Lebistes reticulatus* élevés dans une solution de poudre de thyroïde de mammifère montrent une accélération marquée de la croissance par rapport aux poissons de la même ponte, la réponse des femelles étant plus intense que celle des mâles. Inversement, les jeunes élevés dans une solution de thiouracile manifestent une croissance nettement ralentie. Leur thyroïde apparaît d'ailleurs à l'issue du traitement considérablement hyperplasiée et très active. La différenciation du gonopode s'effectue très précocement chez les animaux traités à la poudre de thyroïde, tardivement chez ceux traités au thiouracile. Enfin M. L. Gaiser (1952) trouve chez la même espèce, que la thyroxine à dose faible stimule le développement des gonades et leur maturation, tandis que la thiourée entraîne un retard à la différenciation sexuelle et à la maturation des gonades, en même

temps qu'un ralentissement de la croissance. Quand les taches de maturité génitale sont atteintes, il semble que la thyroxine accélère la croissance, mais l'expérience devrait être prolongée pour permettre une conclusion ferme. Ainsi, la majorité des auteurs observe-t-elle une action de l'hormone thyroïdienne sur la croissance et la maturation génitale, action qui peut d'ailleurs varier, selon l'espèce envisagée, les doses et le mode d'administration.

Quant aux antithyroïdiens, leur action semble incontestable. Indépendemment des auteurs cités dans le paragraphe précédent, Goldsmith, Nigrelli, A. Gordon, Charriper et M. Gordon (1944) observent que l'immersion de *Platypoecilus maculatus* et *Xiphophorus hellerii* dans une solution de thiouré (antithyroïdien) provoque un arrêt de la croissance et l'absence du développement des caractères sexuels secondaires. Hoar et Bell (1950) observent aussi un ralentissement de la croissance par la thiourée chez le saumon du Pacifique.

Gerbilsky et Žaks (1947) soulignent l'influence très nette de la thyroxine sur le développement post-embryonnaire de l'esturgeon. Dans des solutions de thyroxine, il y a nette accélération du développement des plaques osseuses. A ce propos, il faut citer d'ailleurs le travail de Jakouleva (1949) sur de jeunes larves d'Acipensérides (esturgeons) et selon lequel l'activité sécrétrice de la thyroïde débute dans la vie post-embryonnaire alors que l'hypophyse n'est pas encore fonctionnelle. J. Buser a récemment montré l'influence favorable de la thyroxine et de l'hormone thyréotrope sur la régénération des nageoires des téléostéens.

Enfin il existe toute une série d'expérimentateurs (Landgrebe, 1941; Robertson, 1948; La Roche, Leblond et Préfontaine, 1950) qui ont montré que l'hormone thyroïdienne en ingestion ou en injection entraîne l'argenture des Salmonidés et Robertson (1951) signale l'action mélanoconstrictive des extraits thyroïdiens chez la truite. Ainsi donc très nombreuses sont les expériences prouvant que la thyroxine ou des corps voisins plus complexes tels que des poudres de thyroïde peuvent modifier la morphologie du poisson.

Seulement dans ce genre d'expériences on peut toujours faire l'objection suivante: ce que vous observez, c'est une action pharmacodynamique, ce n'est pas une action physiologique normale. Mais cette objection est levée quand nous voyons apparaître spontanément chez une espèce, à la suite d'une hyperactivité de la glande thyroïde, des modifications que nous pouvons produire expérimentalement par thyroxinisation du poisson.

Ainsi la transformation du jeune saumon de parr en smolt ou smoltification est la conséquence, au moins pour une bonne part, d'une activation de la glande thyroïde, comme l'a bien montré tout un ensemble d'études histologiques, chimiques et biophysiques (emploi de l'iode radioactif). Cette smoltification est caractérisée par un certain nombre de modifications morphologiques et biochimiques: l'argenture, la chute du coefficient de condition ($K = \frac{100\ P}{L^3}$), la chute du glycogène hépatique. Or, ces transformations nous pouvons les obtenir expérimentalement par thyroxinisation des Salmonidés (Fontaine et Baraduc).

Ainsi, dans cet exemple, la thyroxinisation expérimentale et l'activation physiologique normale de la thyroïde exercent-elles des actions comparables sur la morphologie et sur certains métabolismes. D'autres exemples d'ailleurs de cette même corrélation ont été donnés, tel l'allongement des nageoires qui a été vu par divers auteurs, soit expérimentalement, soit spontanément dans la nature, par exemple chez l'anguille lors de sa transformation d'anguille jaune en anguille argentée, tel aussi l'épaississement de la peau.

On a constaté aussi récemment que des préparations thyroïdiennes sont susceptibles de modifier la forme du crâne du jeune saumon parr (La Roche, Leblond et Préfontaine, 1950) et de la truite arc-en-ciel (Fontaine et Baraduc). Rappelons à ce sujet que les deux formes de rouget, *Mullus surmuletus* et *Mullus barbatus*, qui ont été longuement étudiées (Fage, 1909; Remotti, Desbrosses, Olivereau, 1947; Bougis, 1951) et qui furent considérées par certains auteurs comme des variantes endocrines fondamentales d'une même espèce selon l'expression de Fage, présentent une forme de la tête qui diffère — avec d'ailleurs des intermédiaires entre les deux types — ce qui se comprend aisément si l'on admet qu'elles sont dûes à des variations d'intensité du fonctionnement hypophyso-thyroïdien à partir d'un type fondamental. Donc il est incontestable que l'intensité du fonctionnement thyroïdien et de son stimulant hypophysaire retentissent sur certains caractères morphologiques et biochimiques des poissons.

Envisageons maintenant la question suivante: existe-t-il certaines relations entre l'activité de la glande thyroïde et le comportement du poisson?

On peut répondre aujourd'hui par l'affirmative.

Les premiers travaux qui ont apporté des faits précis en faveur de cette hypothèse sont ceux de Harms (1935). Celui-ci a montré que l'administration d'hormone thyroïdienne à des espèces de *Periophthalmus* peu adaptés à la vie terrestre en faisait des animaux à vie terrestre beaucoup plus accusée. Il a même pu réaliser l'amphibiose chez une espèce typiquement marine, *Blennius ocellatus*, en la nourrissant de thyroïde. Cette blennie ainsi traitée sortait complètement de l'eau et restait 8 heures émergée. Au bout de ce temps, elle se replongeait un court moment dans l'eau, puis reprenait ensuite sa place, pour plusieurs heures, sur une pierre complètement émergée.

D'autre part, chez les espèces de poissons qui à l'état larvaire sont exclusivement aquatiques et à l'état adulte amphibies, Harms observe que lors du passage de l'état larvaire à l'état adulte, la thyroïde subit une modification de structure qui en fait un organe plus proche de la thyroïde des animaux terrestres et sans doute plus actif. Il faut rapprocher de ces résultats de Harms l'observation que c'est au moment où l'anguille argentée présente un hyperfonctionnement thyroïdien, juste avant sa migration, qu'elle sort fréquemment de l'eau, courant dans les

prés humides. Cette découverte de H a r m s révèle une action très intéressante de l'hormone thyroïdienne chez les poissons, mais d'une portée assez limitée pour l'interprétation de l'éthologie des poissons puisqu'elle ne touche que les espèces amphibies.

Sur le hareng, B u c h m a n n (1940) a décrit un cycle d'activité thyroïdienne qui peut être lié au comportement, mais qu'il a surtout relié à la métamorphose et au cycle génital sans nous donner sur les sujets étudiés toutes les précisions qui nous permettent de savoir si au moment de la capture, le hareng était par exemple contrenatant ou dénatant. De plus B u c h m a n n interprète de façon parfois inattendue les images histologiques qu'il a obtenues. Il interprète, par exemple, comme signe d'une hyperactivité fonctionnelle de la thyroïde la présence de grands follicules à épithélium très bas et pleins de colloïde, interprétation qui ne peut être maintenue. Toutefois, on peut retenir du travail de B u c h m a n n, certains faits intéressants et notamment qu'un peu avant la fraye se produirait l'élimination de la colloïde thyroïdienne, élimination qui se poursuivrait pendant toute la durée de la fraye et qui peut dans une certaine mesure expliquer la frénétique agitation du hareng se reproduisant et la disparition des graisses et du glycogène hépatique qui brûlent très rapidement pendant ces deux semaines.

Mais dans le cas du hareng, on peut objecter que bien d'autres facteurs internes, et en particulier les fluctuations d'activité des glandes génitales peuvent être rendues responsables de ces variations de comportement.

Plus sûrs sont les arguments tirés de l'étude de deux migrateurs, l'anguille et le saumon, examinés au moment de leur migration d'avalaison. Et voici pourquoi: Dans les deux espèces, cette migration d'avalaison est précédée d'un hyperfonctionnement de la thyroïde (F o n t a i n e et C a l l a m a n d, 1942; B e r n a r d i, 1948; H o a r, 1939; F o n t a i n e et O l i v e r e a u, 1947) qui entraîne d'ailleurs des modifications de robe dont certaines sont comparables dans les deux espèces, telles le dépôt de guanine dans la peau. Mais, ce qui est particulièrement intéressant, c'est que les conditions d'activité génitale sont ici très différentes. L'anguille femelle, par exemple, migre alors que les organes génitaux viennent de commencer à se développer de façon importante. Au contraire, le jeune saumon, le smolt femelle migre avec des glandes génitales au repos. En ce qui concerne le smolt mâle, les états génitaux les plus variés peuvent être observés, les uns présentent des testicules filiformes et n'ont subi aucune maturation génitale au cours de leur vie en eau douce, les autres ont participé à la reproduction des grands saumons en Décembre-Janvier et parmi ceux-ci les uns ont des testicules encore latescents, chez d'autres, les testicules ont considérablement régressé. Ainsi cette variabilité de l'état génital au moment de la migration conduit-elle à penser que les hormones génitales ne jouent pas un rôle prépondérant dans le déterminisme de cette migration d'avalaison.

Au contraire, la thyroïde montre toujours histologiquement une grande activité. L'étude plus approfondie de la thyroïde du jeune saumon, plus approfondie j'entends par des techniques variées chimiques, physiques

(emploi de l'iode radioactif) nous a montré que chez le jeune saumon, il y a hyperfonctionnement thyroïdien intense bien mis en évidence par la cytologie, la chimie et la physique et qui correspond à la smoltification; puis au moment même de la migration, si la glande d'après les critères cytologiques fonctionne avec le maximum d'activité, elle fixe cependant moins d'iode radioactif que pendant la smoltification et comme l'organisme au métabolisme activé, sollicite une production importante d'hormone thyroïdienne, l'hypophyse sécrète en abondance l'hormone thyréotrope. Il est vraisemblable que c'est cette hypersécrétion d'hormone thyréotrope qui entraîne l'agitation motrice qui déclanche la migration d'avalaison. J'ai développé ailleurs (Fontaine, Leloup, Olivereau, 1952) les faits qui nous conduisent à cette conception et ne m'y attarderai pas ici mais ils vous expliquent le titre de cette communication ("La fonction hypophyso-thyroïdienne") car, en réalité, les deux fonctions, la fonction thyroïdienne et la fonction hypophysaire thyréostimulante sont étroitement liées: le fait est bien connu chez les homéothermes et peut être étendu aux poissons car l'histologie, la chimie et la physique nous ont montré la réalité de ces liens chez les poissons. Il semble toutefois qu'elles se manifestent chez les poissons, moins rapidement et moins intensément que chez les homéothermes. C'est ainsi que les modifications histologiques de la thyroïde consécutive soit à l'hypophysectomie (Fontaine et Olivereau (résultats inédits)) soit à l'action des antithyroïdiens ou de l'hormone thyréotrope (Olivereau, 1952) se manifestent plus lentement et souvent moins nettement. Toutefois, dans la plupart des cas étudiés jusqu'ici, on ne peut encore dire si l'activité thyroïdienne est primaire ou secondaire à une hyperactivité hypophysaire. On n'a donc pas le droit de dissocier les deux fonctions avant qu'une étude approfondie de l'hypophyse et de la thyroïde ait permis de le faire.

Mais revenons aux liens existant entre l'activité thyroïdienne et le comportement et apportons maintenant des arguments tirés plus spécialement de l'étude du sang.

Il est un test que de nombreux travaux sur les mammifères ont prouvé être très représentatif de l'activité thyroïdienne, c'est la teneur du sang en iode organique, et en iode dit thyroxinien, c'est à dire entrant dans la molécule de thyroxine ou de triiodothyronine et qui peut être séparé par des caractères précis de solubilité.

Or si l'on dose ces formes d'iode dans le sérum des poissons marins (Leloup, 1949), on observe un lien évident entre leur concentration dans le sérum et l'activité du poisson. Par exemple:—

en mg. pour 100cc. de sérum	Iode protéique	Iode thyroxinien
Rascasse (*Scorpaena scrofa* L.)	7·9	1
Plie (*Pleuronectes platessa* L.)	6	3
Muge (*Mugil auratus* Riss.)	24	14·7
Maquereau (*Scomber scombrus* L.)	26	19·2
Chinchard (*Caranx trachurus* L.)	24·2	17·4

Ainsi puisque la teneur du milieu intérieur en iode protéique et en

iode thyroxinien est très représentative de l'activité thyroïdienne de l'organisme, on peut conclure de ces données et de plusieurs autres qui confirment les quelques chiffres ci-dessus que l'activité plus ou moins grande des espèces de téléostéens marins est liée à l'intensité du fonctionnement thyroïdien.

Si d'autre part, on compare les iodémies des poissons migrateurs amphibiotiques potamotoques capturés alors qu'ils remontent les fleuves pour gagner les frayères c'est-à-dire alors qu'ils jeûnent et en eau douce (2 conditions favorables à une basse iodémie), — si l'on compare dis-je ces iodémies des migrateurs amphibiotiques à celles des poissons holobiotiques — on constate qu'elles atteignent des valeurs plus élevées que celles des poissons holobiotiques et que, de plus, le coefficient de variation des iodémies totales, protéique et thyroxinienne est plus élevé pour ces poissons migrateurs que pour les poissons holobiotiques (Fontaine et Leloup, 1952). Il faut donc admettre que ces poissons migrateurs amphibiotiques présentent un tonus thyroïdien, d'une part

Tableau 1. Iode total, organique et thyroxinien, du plasma des poissons téléostéens (en g. %).

	Iode total		Iode organique		Iode thyroxinien	
	Min.	Max.	Min.	Max.	Min.	Max.
Téléostéens d'eau douce	4·5	46	1	15	1	15
Téléostéens marins	15	91·5	6	35	1	19
Téléosténs potamotoques capturés en eau douce lors de leur migration anadrome:						
Saumon atlantique	36	257	10	800	10	25
Truite de mer	260	676	54	109	65	101
Grande alose	248	2,300	17·2	70	16·8	40

plus intense que celui des espèces holobiotiques, et d'autre part qui présente des fluctuations plus considérables, fluctuations prenant souvent le caractère de véritables crises d'hyperthyroïdie. A ces crises d'hyperfonctionnement thyroïdien, correspondent sans doute ces phases d'agitation motrice si caractéristiques des grands migrateurs (remontée en flèche des fleuves, saut des barrages, etc. . . .).

Enfin, si l'on pratique ces dosages sur le saumon en pleine migration de montée alors qu'il développe une activité maxima, on trouve des valeurs d'iode thyroxinien comprises entre 10 et 25 γ alors que sur les frayères, quand il devient sédentaire la thyroxinémie varie entre 1·2 et 13 γ (Fontaine et Leloup, 1950).

La moyenne est dans le premier cas de 16 γ, et dans le second de 6 γ. Corrélativement, l'étude histologique montre une glande nettement au repos sur les frayères, et au contraire active chez le saumon de montée (Fontaine et Olivereau, 1947).

Toutefois, là encore, on a pu être tenté de tirer argument du fait que l'hormone thyroïdienne n'accroît pas le métabolisme respiratoire du

poisson pour nier son intervention vraisemblable dans l'activité motrice du rhéotropisme, mais il faut songer que chez les mammifères eux-mêmes, Hall et Lindsay (1938) ont montré que l'action de la thyroïde sur l'activité motrice peut être indépendante de son action sur le métabolisme respiratoire de l'organisme.

Ce niveau d'activité thyroïdienne particulièrement élevé chez les migrateurs, les fluctuations importantes de ce niveau prenant le caractère de véritables crises d'hyperthyroïdie viennent à l'appui de l'hypothèse que nous avons émise depuis plusieurs années, à savoir que les changements de milieu des migrateurs sont déclanchés par des hyperfonctionnements ou des dysfonctionnements neuro-endocriniens qui rendent plus aigu le conflit entre l'organisme et le milieu.

Tous les résultats ci-dessus rassemblés[1]) sont donc extrêmement suggestifs de l'existence de liens entre le fonctionnement thyroïdien et le comportement du poisson. Toutefois, on ne saurait évidemment songer à relier le rhéotropisme *exclusivement* à un hyperfonctionnement thyroïdien. Nous pensons que celui-ci est un élément souvent important d'un état sympathicotonique mais il peut manquer ou être au second plan, d'autres facteurs de cette sympathicotonie dominant alors. Par exemple, chez les cyclostomes en migration anadrome, le rôle de l'activité thyroïdienne dans le rhéotropisme semble beaucoup moins important que chez les poissons comme nous l'a montré l'étude du fonctionnement thyroïdien chez la lamproie marine. Mais est-ce une raison pour nier l'intervention de la fonction thyroïdienne dans la migration anadrome des poissons? Nous ne le pensons pas. On sait, par exemple, que l'hormone thyroïdienne n'accélère nullement la métamorphose des Ammocètes alors qu'elle exerce une telle action sur les larves de Batraciens. Nul ne songe cependant à nier l'action métamorphogène de cette hormone chez les Batraciens.

En résumé, ces divers faits d'ordre histologique ou biochimique obtenus, soit sur des poissons marins holobiotiques, soit sur des poissons amphibiotiques prouvent, je crois, la réalité du lien qui unit fréquemment l'activité motrice et l'intensité du fonctionnement thyroïdien, ou plus exactement hypophyso-thyroïdien.

Cependant je suis persuadé que d'autres glandes endocrines et notamment le système surrénalien interviennent aussi dans le comportement du poisson et que, d'une manière générale, l'étude endocrinologique des animaux marins doit éclairer puissamment leur éthologie. Il faut d'ailleurs toujours considérer dans les interprétations que nous sommes conduits à proposer, facteurs externes et facteurs internes, car les facteurs externes peuvent entraîner des variations d'activité des glandes endocrines qui retentissent à leur tour sur le comportement de l'animal.

L'influence de la température et de la lumière ont été depuis longtemps soulignées. Dans mon laboratoire, Mlle Olivereau a montré que, d'après les critères histologiques, le passage d'un poisson marin en

[1]) Note introduite à la correction des épreuves. Nous venons de prendre connaissance d'un travail de W. S. Hoar, D. Mackinson et A. Redlich d'après lequel l'immersion du frai d'*Oncorhynchus keta* dans des solutions de thyroxine accroît l'activité du poisson, sa vitese de nage et diminue sa tendance à se grouper (Canad. J. Zool., **30**, 273—286, 1952, Octobre).

eau douce entraîne une activation de la thyroïde (1948), tandis que le passage inverse d'eau douce en eau salée freine cette activité (1950).

Bougis (1951) pense que l'activation thyroïdienne qui entraîne l'allongement des nageoires pectorales chez le *Mullus barbatus* est une conséquence de la migration en profondeur. Mais quel est le facteur qui intervient?

Les observations de Schwarz (1940) selon lesquelles la vie du têtard sur fond de vase serait particulièrement favorables à l'hyperfonctionnement thyroïdien suggèrent que la nature du fond sur lequel vit le rouget peut influencer l'intensité du fonctionnement thyroïdien. Dans ce cas précis, la glande thyroïde n'apparaîtrait que comme un rouage interne par lequel le milieu retentit sur la forme de l'organisme.

Ces considérations sur lesquelles je ne puis m'étendre montrent l'étendue et la complexité de ces problèmes. L'étude dont je viens d'apporter les premiers éléments est extrêmement longue et difficile, et ne peut être menée à bien ni par un homme, ni par une équipe. C'est un travail qui ne peut aboutir à une construction vraiment solide que si celle-ci est bâtie par les chercheurs de plusieurs pays.

Je n'ai cependant pas l'intention, mes chers collègues, de vous inviter à vous transformer en endocrinologistes, car ce serait une catastrophe pour l'océanographie. J'aimerais seulement que cet exposé vous incite à solliciter les endocrinologistes de vos pays respectifs de s'intéresser aux animaux marins, et à leur poser des problèmes. Déjà nous avons quelques fructueux exemples de cette collaboration. Tout près de nous, dans ce Danemark qui a tant fait dans le passé et qui fait tant aujourd'hui encore pour cette collaboration internationale des océanographes, notre collègue Bruun a montré la voie à des endocrinologistes danois en étudiant avec eux l'anguille femelle et sa difficile maturation génitale. D'autres endocrinologistes danois ont étudié l'endocrinologie des baleines. Il faut souhaiter que ces travaux se généralisent et que grâce aux suggestions émises par les océanographes et aux interprétations proposées en commun par les endocrinologistes et les océanographes, le labeur des endocrinologistes dans le monde marin profite non seulement à l'endocrinologie, mais aussi à l'océanographie.

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Why Study Marine Fish Diseases? [1])

By

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THE interest in freshwater fishes and their diseases has developed mainly because of practical and economic necessities. In Europe it has been a general custom to grow fishes for food, and more recently in America farmers have become interested in growing fishes in farm ponds. In both England and America great interest has developed in hatcheries for sport fishes.

The first studies of fish diseases were made in the restricted natural habitat of the fish growers' ponds or streams. In these environments it has not been uncommon to find epidemics killing fish (B a b e s and R i e g l e r, 1903). Naturally interest increased as the populations of the world increased and fish became used more and more for food. The study of hatching conditions and fish diseases has become a science in itself. Methods have been improved for the control of diseases; particularly since the development of antibiotics and sulfa drugs, much progress has been made in the combat of freshwater fish diseases.

During controlled laboratory experiments, it is not uncommon for fish diseases to occur, but normally in modern experimental laboratories they can be controlled. However, during a study of living organisms in natural habitats, such diseases may not be so easy to observe and are certainly very difficult or seemingly impossible to combat with present methods. Numerous reports have been made concerning the occurrence, study, and control of fish diseases.

Up to the present time the literature has been concerned primarily with fishes from fresh water. A classical book on fish diseases, which summarizes much of the literature to 1920, has been written by P l e h n (1924). The references apply almost exclusively to freshwater fishes.

[1]) Contribution from the Scripps Institution of Oceanography, University of California, New Series No. 629.

The natural environment of a lake, pond, or stream usually provides optimal conditions for the growth and multiplication of microorganisms. Therefore it is not uncommon to find rather large bacterial populations. While many people recognize this, very few know that the same holds true for a marine environment and that the presence of salt is not a limiting factor. Salt water as well as fresh water may be a natural habitat for bacteria and other microbes which can cause diseases in fishes.

Only a few articles on bacterial diseases of marine fish appear in the literature (Moore Alexander, 1912; Aronson, 1926; ZoBell and Wells, 1934; Nigrelli and Hutner, 1945; Rucker, 1949; Hodgkiss and Shewan, 1950). Fungus infections in marine fishes have been occasionally reported (Fish, 1934; Sproston, 1947).

Although approximately 70 per cent. of the earth's surface is covered by the oceans, relatively few scientists are engaged in studying the sea and not many of these are marine microbiologists. Interest has lagged because of the limited obvious practical applications derived from such research and because there are few organizations where specialized training is offered.

Little thought has been given to the study of marine fish diseases probably because the oceans have, until recently, appeared to have almost unlimited resources. But as our populations and need for raw materials increase, we are turning to the seas more and more for food and other raw materials. It is now time to realize that fundamental information for future investigations should be accumulating, even though practical applications may be limited.

Many people have doubted the presence of widespread marine fish diseases. This is quite easy to understand as there are two general reasons why such diseases may not be noticed. The first is concerned with the physical properties of water. The change in refractive index between water and air causes the visual properties of a compound to be changed. Therefore infectious growths on a fish may be seen when the fish is in water but become invisible when the fish is removed to air. To this is added the complication that fishes are not readily observed in their natural habitat closely enough for lesions to be detected.

During the summer of 1952 at the Scripps Institution of Oceanography, Conrad Limbaugh has made an investigation of certain fishes in their natural habitats. Using a diving unit which allows him freedom in the water for periods up to 45 minutes and at depths to 100 feet, he observed that from 5 to 10 per cent. of fishes of several types had lesions involving the scales, tail, and fins. Several of the infected fishes were speared and brought to the surface for bacterial examination. In the air the fishes looked normal and the diver had to point out the places where he had seen the infections. Later examination of the lesions by phase microscopy and by cultural methods revealed that large numbers of bacteria were present. These observations

demonstrated that an observer cannot easily see the infected part of the fish when it is out of water and therefore most lesions may be overlooked in routine observations.

The second reason why fish diseases may not have been noticed is because of natural predation. An infected fish is usually less active and soon becomes prey for its natural enemies. Therefore relatively few diseased fishes are caught, suggesting that they are absent in nature. Mr. L i m b a u g h noted that most fishes with lesions took cover sooner than their healthy neighbours as if they sensed their incapacity.

Careful observations of fishes from three marine aquaria along the coast of Southern California have demonstrated that infections are common, especially during the warm summer months when the water temperature increases. Such infected fishes are sometimes difficult to see and their lesions are not detected by ordinary observations; only by the most careful examination were the infections detected.

Several types of external lesions have been noted in marine fishes in salt water aquaria. It is common to find tail rot or fin rot, a type of disease that is usually slow but persistent. A white cotton-like growth may involve the bases of the scales, which are pushed away from the body, making the integument appear rough in places. Infections in fish eyes cause the lens to become opaque. Occasionally the formation of gas in the chamber of the eye tends to make the eye appear popped. Some fishes are seen in which the eye lens has fallen out as the result of an infection and the socket healed shut. External bleeding of the skin, believed to be caused by bacterial infection, has been observed and appears to cause the death of the fishes. Other infected fishes have been noted to lose their equilibrium and swim in various abnormal positions. The foregoing observations are just a few which definitely indicate that bacterial infections may be prevalent among marine fishes.

In addition to diseases found in mature fishes, fish eggs and larvae may also be attacked by bacteria and allied microorganisms. A h l s t r o m (1948) has reported that up to 45 per cent. of sardine eggs collected during a study of the Pacific coast sardine were abnormal. It is possible that marine bacteria may have been responsible for a part of the abnormal eggs. Significantly, about 65 per cent. of the known species of marine bacteria attack protein. Recent experiments by the author suggest that bacteria may produce abnormal changes in sardine and flatfish eggs.

Why should marine fishes be studied for diseases? This question has probably been asked at the initiation of most research projects which have no apparent immediate application. But there are many reasons why a study of fish diseases should be undertaken. Such studies might help to explain why some fishes have almost disappeared from certain oceanic areas. Although hatcheries for marine fishes, except those that migrate from fresh water to the sea, have been established in only a few countries, the future may see the need for more such stations. If so, a knowledge of fish diseases would be invaluable. Because of the lack of trained personnel, very little work is being done with diseases in

marine fish hatcheries in spite of many known instances of bacterial infections.

As a result of diseases and the lack of knowledge for their control, many valuable fishes are lost in marine aquaria each year. During the summer of 1952 one aquarium on the west coast of California lost a large part of the fish stock because of diseases. Many valuable fishes could have been saved if the aquarium keepers had known how to combat the infections.

It is likely that certain diseases are carried into aquaria by newly caught fishes, especially those that may have been injured during capture. The practice of isolating new fishes for certain periods of time is of great importance to the maintenance of a healthy aquarium. Information regarding the length of isolation and prophylactic treatments of marine fishes is very scanty and poses an interesting problem for the properly trained microbiologists.

Among the few reports available concerning the occurrences of human diseases spread by marine fishes and crustaceans is a report written by Sheard and Dicks (1949) on infections of *Erysipelothrix*. Recent experiments by the author on known strains of *Erysipelothrix* have shown that the organisms grow well in sea water medium. This would suggest that these organisms are capable of free distribution in the sea and may be a potential human pathogen. Aronson (1926) reported the occurrence of spontaneous tuberculosis in three species of salt water fishes. The organisms were different from the avian, human, and saprophytic Mycobacterium.

Little is known about the occurrence and scope of marine fish diseases. It seems certain that many marine microbes may be potentially pathogenic for fish, so that when the fishes are injured or their resistance lowered, these microbes may produce infections. Interest has been developing during the past few years, but in general, personnel, facilities, time, and funds have not been available for sufficient specialized research in the marine field. As interest in the marine environment increases, it is necessary for research to be conducted even in the more narrow branches. It is hoped that more interest will develop in the future as our daily needs demand that the oceans be exploited for their wealth of raw materials.

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Fishery Management and Research.[1])

By

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THE most populous part of Canada is in southern Ontario, cradled between Lakes Ontario, Erie, and Huron. Less than 160 years ago, planned settlement of the region was begun with the landing of an Englishman, Col. Simcoe, at what is now Toronto, where he found one European living near some Indian wigwams. His plans included provision for a university. It took fifty years for this to come into being and in this university, at Toronto, the development of knowledge particularly related to fisheries did not begin until another fifty years had passed. Robert Ramsay Wright as a young man from Glasgow took the chair of Natural History in 1874, and by 1884 he and his students had produced a classical monograph on the anatomy of the catfish, *Amiurus*. He had become Professor of Biology in, and Secretary of the Board of, the School of Practical Science, established in 1878, which provided for practical work in biology. He assisted the Ontario Game and Fish Commission of 1890 and wrote the part of its report dealing with fish, thus bringing biology into the service of fisheries. In his recommendations, he urged extension of the current fish culture, consisting of the hatching and planting of small fish. Little more than ten years later, that is, about fifty years ago, one of Wright's students, B. A. Bensley, started a Great Lakes fishery research station on Georgian Bay, where in 1904 he introduced me to such research, with study of plankton, fish breeding, commercial fishing, and sport fishing. The expansion of fisheries research under government and by universities since then has been very rapid in the setting of scientific advance by western civilization during the period.

[1]) Originally this paper was prepared, on request, for a symposium or conference on Great Lakes fisheries research under the auspices of the Research Council of Ontario.

If our efforts, which have included the whole of my active life, have failed in effecting sound fishery management, I do not propose to apologize for fisheries research. It needs no apology. Very substantial scientific progress has been made. But it has not been enough. The reason for this seems to be that conceptions which have been governing thought and action are not firmly established in fact.

Conceptions for Management.

High reproductive rate and fishing.

The high reproductive rate that obtains in most fishes, a female producing thousands or even millions of eggs, has certain implications. No matter what the rate of multiplication of an animal may be in nature it leads sooner or later to a saturation with the species of any environment that is suitable. Thereafter the mortality is inevitably high if the reproductive rate is high. A high death-rate in fish is, therefore, a necessary concomitant of a high breeding rate. This permits man to remove very large proportions of populations of fish in suitable environments without affecting future generations of the fish. It gives also the likelihood that fishing will never be so intensive as to decrease the take of fish in the long run, except where practically the whole stock can be easily removed.

Belief that restriction of fishing will increase the long-term yield has been very general. Such possible increase in the long-term yield should not be confused with the better fishing (greater take per unit of effort) which restriction in fishing has been clearly shown to effect. There needs to be analysis of the situation to separate the various possible effects and thus to avoid confusing them. In particular, natural fluctuations in abundance of fish, which have been definitely demonstrated to be prevalent, should be clearly distinguished from any effects of fishing. Unless this is done, increase in yield does not constitute clear evidence of being an effect of restriction.

To illustrate the fishing possibilities that high reproductive rates may permit:— If two fish, male and female, produce 2,000 young (an average Miramichi female salmon yields over 8,000 eggs) and if the mortality which is inevitable is uniform throughout life to give a pair of adults five years old to produce again 2,000 young, over 80 % of the fish must die in each year. There could seemingly be a fishery that takes 1,000 underyearlings, 200 yearlings, 40 two-year-olds, and 8 three-year-olds, and a natural mortality among those left of 60 % without affecting maintenance of the stock. Such a fishery removes 50 % of a stock which must decrease 80 % in any case. Failure of clear evidence that restriction in fishing increases the long-term yield might, therefore, be expected.

Planting of small fish.

If there is an abundance of small fish from a high breeding rate, so that most of them must die, it is foolish to plant small fish.

I have considered that an effort should be made to find situations in which the planting of small salmon could be effective. Its uselessness for the Margaree River, which we investigated intensively from 1934 to 1938, was apparent. During the past twelve years, we have investigated the possibilities with planting experiments in the Petitcodiac River of New Brunswick, in the Duffin Creek of Ontario, and in the Shubenacadie Lake system of Nova Scotia, all of which have, or had, native salmon and seemed through absence or scarcity of small salmon likely to benefit from the planting of small salmon. In no case has there been evidence of success in producing or benefitting a fishery. Where fishery and fish had disappeared the small fish did indeed survive and grow well in waters suitable for them, but no fishery resulted. Where the fishery was slight and conditions for natural spawning and rearing were very poor, no improvement in the fishery could be seen. Even rearing of the young through the stream stage (parr) and planting them as smolts in the lake where they are fished has given at best a fishery use of only 0·34 %. Around 1,250 lb. of 2-oz. two-year-old smolts that were planted gave only about 55 lb. of 1- to 2-lb. four- and five-year-old fish to anglers.

Conservation of small fish.

If there is an abundance of small fish from a high rate of breeding, it is foolish to prohibit moderate use of them.

Conservation of small fish has been quite general in Canada, being embodied in many regulations. We have been unable to learn of any substantial basis for the practice. The taking of small herring for bait and for manure in the international Passamaquoddy region of the Bay of Fundy was condemned over a century ago; but starting in 1876, they came to be fished most intensively because of their high value when canned as sardines. After more than seventy years of such use, the small herring continue to be plentiful and have been giving twice as high a poundage as when the fishery was confined to the large fish. This demonstrated clearly the foolishness of the desired restriction.

The result from planting small salmon which has already been given provides no basis for conserving the small fish. Another test in which salmon that had completed four years of growth were tagged and planted gave the result that 241 lb. of small contributed only $2\frac{1}{2}$ lb. of large (five year olds) to the angling. There have been similar results with trout. The best case for conservation of small fish that has come to light in our salmon investigations is for the smolts of the Moser River, N. S. Of these smolts, 10 % survive to become grilse the next year and each fish increases in weight about 2,300 % (2 oz. to 3 lb.). Since at best only 25 % of the grilse are captured, it takes $12\frac{1}{2}$ lb. of smolts to give $7\frac{1}{2}$ lb. of grilse to the anglers, which is not a very favourable result. Testing the value of saving small fish might well precede consideration of the value of planting small fish. If conservation of small fish is not worth while, it is surely not worth while to go to the expense of producing them for planting.

Protection of spawning fish.

If each pair of fish produces thousands of young, there is no need for many spawning fish and it is foolish to restrict moderate use of them.

There has been general belief that spawning fish should be protected and this has been embodied in many regulations. In the middle of the nineteenth century, an officer was appointed by the colonial government of New Brunswick to prevent fishing on the spawning grounds of the herring of the Passamaquoddy region, which were clearly defined on the outer side of Grand Manan Island in the mouth of the Bay of Fundy. Development of very intensive fishing for small herring for canning as sardines reduced the numbers of spawning herring to a very low level by 1890, but the numbers of the small were evidently maintained. Protection of the spawners was abandoned in 1918 without any noticeable effect on the quantities of herring that were taken.

The only fishery for sea salmon is when they have ceased feeding and are roaming about before spawning in streams. They are particularly susceptible to capture when passing through the narrow entrances to rivers. We have been trying for a long time to discover definite evidence that, or to learn of clear cases in which, so many salmon have been taken as to affect the numbers of fish in the next generation. We do not know of any case in North America. A case (the Conon River) has been reported for Scotland, in which the numbers of salmon increased abruptly the proper number of years after fishing was stopped, this fishing having included use of a trap that could take practically every fish that might ascend. Similar cases have been recently reported for northern Norway. The conclusion seems to be justified that overfishing to affect the next generation occurs only when the stock can be fairly thoroughly removed. Experience seems to show that this is possible only in smooth-bottomed ponds and in narrow channels through which all the stock must pass, but certainly not in lake or sea.

Wandering versus homing.

The migrations of fishes have been generally believed to be purposive movements between breeding grounds and feeding grounds. This has been visualized as a foraging for food, in which the fish learns the way for later return home. A substantial basis for this belief has never been furnished. Investigation of the salmon as an outstanding example of fish that feed and breed in very different waters (the sea and river rapids) has failed to reveal any ability of the fish to direct its course over the earth except when near the bottom. Its success in migrating between breeding grounds and feeding grounds has been found to depend upon its being directed by the environment when merely wandering and upon being transported by currents. The current of its river not only transports it from its birthplace to feeding grounds in the sea, but also directs its course back when it becomes fat and wanders vigorously. Homing is a reality, but it is very limited in character. It is the end of wandering rather than a directive factor.

While for management the important matter is where the fish goes, not how it gets there, only sound knowledge of how it gets there will enable us to predict where it will go and when. An understanding of the mechanism of migration becomes, therefore, of great importance for management.

Ecads versus races.

In the nineteenth century, local kinds of herring and other fish came to be considered as races in the mistaken belief that their distinguishing characters, such as numbers of vertebrae, must surely be hereditary. Investigation has shown, however, that these are the effects of the environment, temperature at a crucial stage in the development of the individual determining how many vertebrae it will have. A kind that is the effect of the environment on the individual during its development is an ecad, not a race. Races of herring or of other species of fish doubtless exist or could be developed by selection in breeding, but they should not be confused with ecads.

Various differences have been noticed between the salmon of the different rivers, for example in the ages and sizes at which they return, and there has been general belief that these indicate more or less distinct river races. Differences in the time of the year at which salmon return to rivers have given rise to belief that there are early running and late running races even in the one river. The fact that some salmon mature in lakes without descending to the sea and that they differ considerably in colour and otherwise from sea salmon was considered as justifying their being made a separate subspecies with a non-migratory habit. Our investigations have failed to reveal that these kinds are in any way hereditarily different and no evidence has been adduced that they are, so that warrant is lacking for considering them to be races or subspecies. There is definite evidence that they are produced by the environment and are, therefore, ecads. The environment clearly has a very marked influence on the character and on the behaviour of the fish.

Belief in races has not infrequently governed thought and action in fishery management. It should not be permitted to do so without evidence of hereditary differences.

Local peculiarities.

Since the environment acts upon the fish in so many ways and plays such an important role in determining their character and their behaviour, and since the environment is so variable, environmental differences from place to place need to be taken into account for effective management. Unfortunately there is strong desire among those concerned with fishery management to avoid what might be interpreted as favouritism, by having uniform measures in management. Also there is a strong desire among those engaged in research to reach conclusions of general validity. Both of these desires run counter to the actuality of great local and even temporal differences in the environment, which may require peculiar local and temporary management.

Facing this situation, we find that, while data from which conclusions may be drawn are most important, refined mathematical treatment of data in accordance with the theory of probabilities, and with the object of developing the best general policy in management, is unsound, as glossing over important differences that should be taken into account. The task on the research side is to elucidate the differences, not to ignore them by resort to the theory of probabilities.

Clearly Successful Management.

Fishermen naturally insist on regulations that permit fishing to be worth while. Except for this, practically the whole of current fishery management is of questionable character as based upon conceptions that are not firmly established in fact. Such should be considered only as experiments, of which the results should be determined. To continue such practice without determining results is to run the risk of responsibility for utterly useless or even harmful procedures.

The course that should be taken to develop clearly successful management is, not to act on conceptions that may have no substantial basis, but to take procedures that are based upon the facts of research and that may be shown to produce the desired results, and then to attempt to develop them so that results shall warrant the costs that may be involved.

For example:— It has long been desired in Canada to increase the stocks of salmon and trout. Experiment showed that nearly all of the small trout planted in certain streams disappeared within a few summer months. Further experiment in one of these streams showed that the disappearance was due mainly to predation by large fish and by birds. Study revealed that in the Margaree River of Cape Breton Island mergansers and kingfishers were subsisting almost entirely on young salmon and trout where these were practically the only fish present. Rather thorough elimination of these birds in such a locality for a full year gave 120 % increase in the numbers of salmon smolts descending and was followed the right number of years later by approximately a doubling of the catch of salmon on the Margaree coast. Other rivers studied have shown quite different conditions. The control of birds on the Margaree or similar rivers, which has thus been shown to produce the desired results, remains to be developed into an economical procedure.

Re-orientation of Research.

As dealing with unknown quantities, research is not something that can be safely directed. The investigator who tackles a problem should be free to choose his own tools. Nevertheless, amid the limitless possibilities of what shall be investigated and of methods to be used in the investigation choice must be made. Good judgement in the choice may greatly better the prospects for solving the problem. It should not be expected that funds allocated for fishery research be made available except for problems that are seen as bearing on fishery needs, and it is

natural that most support should be given for attack on the problems seen as being most important.

There seems to be definite need for re-orientation if we are to have research that will quickly develop clearly successful management. Money and effort cannot be considered to be well spent on attempts to improve or even to test procedures of questionable usefulness that are based upon conceptions not firmly established in fact.

There seems to be no good basis for restricting fishing in order to increase the long-term yield. Yet in connexion with the Pacific halibut experiment "it has often been said that the halibut regulation presents the only definite case of sustained improvement of an overfished deep-sea fishery" (W. F. Thompson, *J. Cons. Int. Explor. Mer*, **18**, 2, 1952). How should the results of this experiment be judged? In it the Pacific halibut fishery that is shared between the United States and Canada has been controlled by the International Fisheries Commission for more than twenty years. The experiment was based upon, and has been a test of, a theory of fishing (W. F. Thompson, *Rep. Inter. Fish. Comm.*, **12**, 1937). Belief in the theory and admiration of the experiment may prevent criticism, and result in general acceptance of what requires more evidence.

The great difficulty in evaluation rests in the complexity of the matter and in the failure of the argument advanced for the validity of the theory to elucidate that complexity. The improvement mentioned may mean either a greater take of fish or greater ease or success in fishing (greater take per unit of effort). These should be clearly distinguished. The first question to be answered is, Has restriction in fishing increased the take; that is, has it been possible to take more by fishing less? This can only be a long-term phenomenon, since in any one season the more the fishing the greater the take. Less fishing may possibly give more fish to take in later years through more growth from small to large and through more breeding. The fishing facts (Thompson, *op. cit.*, 1952) show on the whole a general rise in take with a general fall in effort. This definitely supports the theory. The argument is no stronger when the facts are expressed as a marked rise in ease of fishing or as the involved relation of effort to ease ("relationship of number of sets of gear and catch per set"). It has been maintained, however, (M. D. Burkenroad, *Bull. Bing. Ocean. Coll.*, **11**, art. 4, 1948) that the rise in take may represent a natural rise in abundance. Since, unlike the theory of fishing, natural fluctuations in abundance of fish are well attested and are evident in the takes of halibut on both sides of the North Atlantic, a natural change in the abundance of the Pacific halibut is to be expected. It is unwise to brush aside, as Thompson does, this probability of a natural fluctuation in abundance of the halibut affecting the takes of halibut with which he deals. Whether in medicine or in fishing, an attempt to remedy an unfavourable situation is usually made at the low point in a fluctuating condition and the doctor or the fishery manager gets credit for his treatment of the case from the upward rise, which was coming without the treatment.

The Ristigouche Salmon Club of northern New Brunswick and Quebec was able to claim success in its attempts to increase the salmon stock when there was a general rise in the take over a period of more than twenty years. But then there came a dramatic drop in the take, which showed that factors were operating of which no account had been taken. Judgement should be reserved as to there being significance in the correlation between decreased effort and increased take in the Pacific halibut fishery.

The second question to be answered is, Has restriction in fishing increased the take per unit of effort, that is, has the ease in fishing depended upon the amount taken? To be different from the preceding, this question must be restricted to the one season. Thompson (*op. cit.*, 1952) argues in this connexion the importance of the reciprocal or inverse relationship between the effort (number of sets of gear) and the ease (catch per set) of the fishing. As was appreciated by S. J. H. (*Journ. du Cons.*, **17**, 3, p. 321, 1951), the limits set on the yearly take automatically bring about this relationship. When the market or the Commission sets a limit on the amount to be taken, good fishing for any reason whatsoever in a given year will result in the quota being filled with relatively little effort, and conversely poor fishing will result in relatively great effort being expended. Thompson's argument that, through an effect on the population, restriction of effort gives greater ease, as evidenced by the inverse relationship, falls to the ground when the setting of a limit to the take automatically results in the ease reducing the effort. Moreover, it should be pointed out that while abundance undoubtedly affects the ease of fishing or catch per set, it is unwarranted to assume that the latter "represents the magnitude of the stock of fish". That the facts with which he deals can reveal the "Condition of Stocks of Halibut in the Pacific" is open to serious question. However, it is to be expected that on the whole with less fishing there will be greater ease in fishing. The greater the number of fish taken from the water, the poorer the fishing is apt to be until these have been replaced. It may be doubted whether the experiment was needed to determine an effect of this kind, or that for better fishing fishermen should wait until the time in the season when the fish can be most easily caught, another idea that is included in the theory.

The conclusions to be drawn from the Pacific halibut experiment remain quite uncertain and the validity of the theory of fishing to account for the facts is still in doubt. It is to be hoped that there may be separate elucidation of the various factors that affect this fishery.

With no overfishing to affect the long-term yield, the fishermen in order to improve their economic position need to choose between (1) restricting their fishing so as to increase their take per unit of effort and (2) making their efforts more effective. The latter may be aided by research. We need knowledge for predicting where and when desired fish will be sufficiently concentrated for economical capture, and also knowledge for their more effective capture. Basic research is requisite on the behaviour of the fish in order to reveal the factors that determine

their whereabouts and their capture. The ocean and the great lakes are inexhaustible reservoirs of food for man, but their inexhaustibility is owing, not to the fish being in unlimited amount, but to the great difficulty in capturing the fish when scattered through the water. There seems to be no prospect of man making more than slight and temporary changes in such large bodies of water or in their fish populations. Effort in fishing, management, and research should be directed toward getting what we can from them.

It is another matter with ponds and streams. Man can exercise a fair measure of control over them and over their fish populations. For fish with a high reproductive rate we need to be concerned with little more than providing conditions that are suitable. Research to determine what these conditions are is badly needed. For each kind we should discover what is requisite for its survival, its growth, and its reproduction. For those that are free to wander we should discover what determines where they will be found and how best they can be caught.

What Research?

Biologists as a whole, including those of past generations, cannot be absolved from responsibility for whatever fishery management there has been. If practice in that management has been almost wholly without substantial basis, and if the ideas governing that practice are proving to be illusory, we biologists must expect to be blamed. It will not do for us to take shelter behind the contentions that the subject is extremely intricate and that the most pertinent facts are very hard to get, true as these may be. It will not do for us to ask for another fifty years or even ten years in which to demonstrate that we can be of real service. The fishery people who are primarily and vitally concerned with the practice have a right to demand, as they are beginning to do, that fishery research provide at once some firm ground upon which they can walk in managing the fisheries. What research will do this?

Requested research.

Since the research is for the fisheries, specific requests from those engaged in the fisheries should be considered first and brought into proper perspective for effective action. Each request should be clearly formulated as a question or questions to be answered. The course to be taken and the probable time required for answering each question should be made clear. At least annually the progress made toward answering each question should be reported. On the basis of current knowledge, we biologists should place researches that are to answer specific questions in more or less distinct categories for most effective handling.

Determining aspects.

It seems that two over-riding aspects of the situation need to be appreciated by being clearly expressed. (1) When it lacks substantial

basis, the age-long fear that overfishing may reduce the long-term yield should be disregarded and effort in research directed toward getting more fish economically. (2) Each fish and each locality are more or less peculiar, so that each fishery will require more or less peculiar treatment for effective management. This runs definitely counter to the uniformity that is socially so desirable. Research as well as management should be more or less a piecemeal affair.

Substantially directed research.

The various fisheries have substantial economical bases or they would not continue. Research to extend them is thus substantially directed. Knowledge that will reduce the cost of capture and knowledge that will increase the value of the fish caught are required.

To reduce the cost of capture. For any particular fish in any particular body of water, the questions to be answered are:— How can it best be caught? Where can it best be caught? When can it best be caught? To answer these, we should discover (1) the factors that determine capture of the fish and (2) the factors that determine where the fish will be.

To increase the value of the fish. For any particular fish, the questions to be answered are:— What persons would buy the fish in what condition, in what quantity, and at what price? For any particular fish in any particular body of water, the question then to be answered is:— How can the fish best be handled and transported to furnish the buyer with what is most desired and at a satisfactory price?

Since the quantities of fish available frequently fluctuate considerably from year to year, a basis for predicting what the quantities will be in any particular year is desirable, so that the fishermen may plan accordingly.

To predict quantities of fish. For any particular fish population, two questions require to be answered:— (1) What are the present quantities that will be available for capture in one or more years? (2) What factors are determining the quantities of the fish and how are they changing?

That different fisheries may be depending more or less upon the same stock of fish has been well established. The extent of this may be overestimated.

To clarify conflicts between diverse fishery interests. This question should be answered:— To what extent would the fish taken in any fishery of which complaint is made be used otherwise if not so taken?

Testing possibilities.

There may be demand for research to develop or test possibilities that those engaged in the fishery consider to be of importance. Although the planting of small fish, the saving of small fish, and the protection of spawning fish may not have a substantial basis, there may be strong desire on the part of fishermen to have research carried out on them or on some other possibility of benefitting the fishery that has not been

shown to have a substantial basis. If so, there is no reason why the research should not be done so long as the limitations and implications of such research are clearly understood.

General fisheries research.

A general investigation of a particular fishery in order to develop varied knowledge for managing it has considerable value and may have very great value. Its very vagueness makes any judgement concerning it quite difficult. When both universities and fisheries research stations are conducting such research, there is a regrettable situation. It tends to be academic research that masquerades as fisheries research through having a slight fishery coating. As such it is neither basic enough to be justified from the academic standpoint of the university, nor sufficiently directed toward fishery practice to warrant its having a fishery label.

Basic research.

Experience has shown that research directed toward practical objectives in management reveals great need for basic knowledge of the fish and of their environment. Some of the funds for fisheries research can well be devoted to basic research on fish and on their environment. The amount and directions of such research seem limitless. In giving fisheries support to any basic research, there should naturally be judgement, first of the pertinence for fishery objectives of the direction of the research, and second of the progress made in developing scientific knowledge. Results to affect fishery practice should be taken and worked out by those engaged in fisheries research.

It will be obvious from what has already been stated that basic knowledge is required of the behaviour of the fish as determining their capture, their location, and their survival. What determines their breeding and their growth is also of importance. All these depend upon the environment as well as upon the fish, and knowledge of the dynamics of the physical environment of the fish that affect their behaviour should be obtained.

Fish culture.

No prospect is seen of its being feasible to affect particularly the abundance of valuable fish in large areas and thus have for them anything that might be considered as fish culture. Measures for practical control of the fish or of the conditions in such areas would be expensive. However, the fishes which are susceptible to considerable control are those that spawn in tributary streams. Lampreys and smelts may be in this category, their control in the Great Lakes being demanded.

It should be realized that in China and India there has long been successful culture of fishes in confinement, with extremely high productivity per acre. In so far as such culture is required elsewhere, there is substantial basis for research to develop and extend it within the limits set by the conditions. Its extension to waters too large for the controls that are found to be advisable is not to be expected.

Conclusions.

The object of each research should be clearly defined as the answering of a specific question or questions.

Major effort in research should be directed toward reducing the cost of capture of fish and toward increasing their value.

In so far as it may be requested, research should be conducted to permit prediction of the quantities of fish.

In so far as it may be requested, the extent to which the fish taken in any particular fishery would be used otherwise if not so taken should be determined by suitable experiments.

Research in developing or testing mere possibilities of successful practice in management should be limited to those for which there is an over-riding demand.

General investigation of a particular fishery should be discouraged except as a preliminary measure prior to decision on the specific object of the research.

Support should be given to the most promising basic research on fish and on their environment, as may be seen likely to provide knowledge of the behaviour of the fish in relation to their capture, their location, their survival, their breeding, and their growth.

As soon as feasible the best possible effort should be made to initiate a system of local fishery management to consist of continuing research to apply all available knowledge to the local dynamic situation. This needs to be done by a particularly well qualified man who spends his whole time in co-operation with those concerned with the fishery in studying the dynamics of the water, the fish, and the fishery, for intelligent action by those concerned in making the most of the local fishery possibilities. Such a man would be a fishery investigator and manager.

Forecast.

The facts and logic of the situation seem to make it inevitable that research must be along the lines indicated if there is to be success in fishery management. The magnitude of the research in progress is so great that its momentum prevents any easy diversion of its direction. It may, therefore, take fifty or a hundred years for it to be well directed. My experience in research from university instruction to actual fishery management convinces me that the proper directions for quick success could be taken at once if there were the will to do so.

Some Observations on the Principles of Fishery Regulation.

By

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SINCE 1947, Mr. S. J. Holt and the present author have been engaged in research on the theory of fishing. The following is a paper read at the General Meeting of the International Council in Copenhagen, 1952, giving some of the main conclusions reached, with special reference to the North Sea demersal fisheries. A full account of these investigations will be published shortly in the *Fisheries Investigations* Series of the Ministry of Agriculture and Fisheries.[1])

Introduction — statement of the problem.

During the first half of the present century the history of the development of the North Sea demersal fisheries has provided a practical demonstration of the behaviour of an unregulated fishery. The main feature is that a rough balance has been set up between the fishing activity on the one hand and the natural productivity of the stocks on the other, but the level at which this steady state was maintained has on the whole been unfavourable to man, many fishing industries being forced to operate at an undesirably low economic level.

It is equally clear that factors exist in a fishery without external regulation, particularly the fundamental competitive element in fishing, which make it difficult, if not impossible, for the industries to regulate themselves to achieve a more favourable balance. Nevertheless, the evidence resulting from the cessation of fishing during the two wars suggests that the decline in productivity and economic conditions since the beginning of the century is almost certainly reversible.

These observations constitute, in effect, the starting point of the investigations which have led to the conclusions presented in this paper. Our basic problem is to gain an understanding of the mechanism which

[1]) Beverton, R. J. H., and Holt, S. J. (In Press). "On the Dynamics, Exploitation and Conservation of Fish Populations". Fish. Invest. Ser. II. A preliminary note was published by Hulme, H. R., Beverton, R. J. H., and Holt, S. J., in *Nature*, Vol. 159, pp. 714—715, 1947.

enables a fishery to reach a steady state and of the factors contributing to it, with special reference to the factors which are potentially within man's power to control, namely, the amount and kind of fishing activity. The final objective is to determine the balance which is most advantageous to man, and to define the regulative measures which are required to achieve it.

The answers to these questions will of course vary in detail with each particular fishery which is considered, but our enquiry has led to certain general principles which we believe can provide the framework within which measures for the regulation of the North Sea demersal fisheries can be most effectively devised. It is to present these principles as concisely as possible, rather than to discuss the practical details of regulation, that is the main purpose of this paper.

Method — the development of a theoretical model of an exploited fish population.

The only satisfactory method of tackling this problem in the North Sea fisheries — and probably in most others — is to set up a theoretical model of an exploited fish population which represents as faithfully as possible the fishery in question. A study of the properties of this model should then lead to a fuller understanding of past events, and form the basis of future predictions. This is the method used by many authors, notably by Baranov (1918), Russell (1931), Graham (1935), and Ricker (1944). The simplest form of model used in the present investigations is most similar in principle to those of Baranov and Ricker, though it differs in certain important details. It is developed by considering first the survival of a year-brood from the age, t_ϱ, at which it is recruited to the area where fishing is in progress, when it numbers R fish in all. At this age the fish are liable to encounters with the gear, but in general will be too small to be retained by the meshes, and their numbers will be reduced by natural mortality alone. At some later age, $t_{\varrho'}$, depending on the selective properties of the gear in use, the surviving fish will be retained if they enter the net, and the brood is said to have entered the exploited phase of the life-cycle. Hence the number of fish entering the exploited phase at age $t_{\varrho'}$ is

$$N_{t_{\varrho'}} = Re^{-M(t_{\varrho'}-t_\varrho)} \quad \ldots\ldots(1)$$

where M is the instantaneous natural mortality coefficient. At any subsequent age t greater than $t_{\varrho'}$, the brood is being reduced in numbers by both natural and fishing mortality, although each surviving fish is increasing in weight by growth. If the weight of an individual fish at age t is denoted by w_t, and the number surviving to this age by N_t, the total weight of the brood at age t is $N_t w_t$. Thus the rate of yield from the brood is $FN_t w_t$, where F is the instantaneous fishing mortality coefficient and is proportional to the fishing intensity. The total yield in weight, Y_w, obtained from the brood throughout its life is therefore the integral of the function $FN_t w_t$ over the exploited phase, that is,

between ages $t_{\varrho'}$ and the end of life, which for convenience is taken as some high age t_λ. Thus we have

$$N_t = N_{t_{\varrho'}} e^{-(F+M)(t-t_{\varrho'})}$$

and substituting for $N_{t_{\varrho'}}$ from (1) enables the equation for yield to be written in the form

$$Y_w = FRe^{-M(t_{\varrho'}-t_\varrho)} \int_{t_{\varrho'}}^{t_\lambda} w_t e^{-(F+M)(t-t_{\varrho'})}\, dt \qquad \ldots.(2)$$

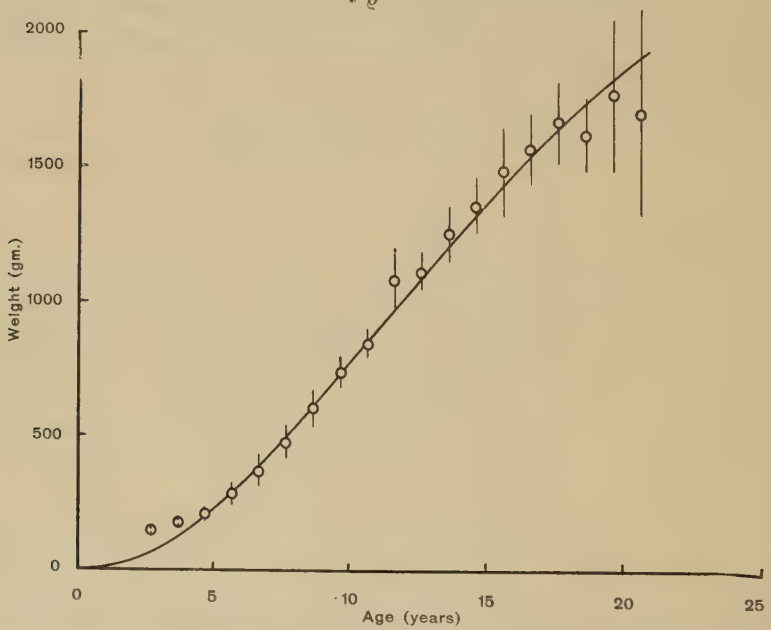

Figure 1. Growth in weight of North Sea plaice, with the fitted Bertalanffy curve. The departure of the first three points from the curve is due to sampling bias.

For the growth function w_t we use a modification of the equation developed by von Bertalanffy (1938), viz:—

$$w_t = W_\infty \left(1 - e^{-K(t-t_0)}\right)^3 \qquad \ldots.(3)$$

where W_∞, K and t_0 are constants. This equation is not empirical but is based on physiological concepts, and has been found to give a satisfactory representation of the growth of many species of fish, the fit to the weight-at-age data of North Sea plaice being shown in Figure 1. Substituting (3) in (2), and integrating, gives the final yield equation

$$Y_w = FRW_\infty e^{-M(t_{\varrho'}-t_\varrho)} \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\varrho'}-t_0)}}{F+M+nK} \left(1 - e^{-(F+M+nK)(t_\lambda - t_{\varrho'})}\right),$$

where $\Omega_0 = +1 \quad \Omega_1 = -3 \quad \Omega_2 = +3 \quad \Omega_3 = -1 \qquad \ldots.(4)$

This differs from the yield equations of Baranov and Ricker in two main respects, (a) that recruitment is defined as the process by which fish enter the fishing area, and is thus distinguished from entry to the exploited phase and hence the catch, (b) that the growth function used gives a fit to data over a wide range of age, and can be made the basis for the analysis of relationships such as that between growth, food consumption, and population density. Neither of these requirements is satisfied by the cubic equation used by Baranov or the exponential of Ricker. Our introduction of von Bertalanffy's growth equation has already been adopted by one worker in this field, namely R. Jones, of the Marine Laboratory, Aberdeen, in a paper read at the 1951 meeting of the International Council at Amsterdam.

Use of the theoretical model.

It is well known that in fish populations the magnitudes of the recruitment, natural mortality, and growth fluctuate considerably from year to year, but the fact that fisheries tend to reach a steady state when the fishing intensity is stabilized suggests that for the most part the magnitudes of these factors fluctuate about roughly constant mean values. Since we are primarily concerned with using the theoretical model formulated by (4) to investigate steady states, it is therefore sufficient to treat the population parameters, i.e., those of recruitment, natural mortality, and growth, as constants, their actual magnitudes being in fact the mean values found from data. For example, if we suppose that R fish are recruited each year, (4) gives the *annual* yield from the population in the steady state as well as the yield throughout the life of one brood; but with the number of recruits fluctuating about a roughly constant mean value over a period of years, then (4) gives the mean annual yield during that time.

Used in this way the model can establish the main dynamic properties of a fishery and can indicate the first steps which are required to regulate it, but for making accurate predictions of the regulation required and of its probable effects it is necessary to take other factors into account. Of particular importance here is the variation of the parameters with population density, since the latter will change if either the fishing intensity (i.e., the value of F) or the selective properties of the gear (i.e., the value of $t_{\varrho'}$) are altered. Introducing phenomena of this kind makes the model more realistic and gives it the properties of "self-compensation" which are characteristic of natural populations, though much greater demand is made on the data. However, enough progress has been made in this direction to establish that the general conclusions to be presented below, which are mainly based on the simple model with constant parameters, are not invalidated if more complex phenomena, such as density dependence, are introduced.

Although we are concerned here with general principles of regulation rather than with specific proposals for a particular fishery, nevertheless the model must in the first instance be applied to a particular fish

population, and the parameters estimated from research data and commercial statistics during a period when it was in a reasonably steady state. For the North Sea, a period of ten to fifteen years immediately prior to the second world-war satisfies this requirement, enough data being available to estimate the parameters for the plaice and haddock with some accuracy and to give approximate estimates for the cod and sole. Investigations have shown that the data for the *plaice* are sufficient for purposes of illustration, and in what follows reference will be made primarily to this species and its associated fishery in the North Sea.

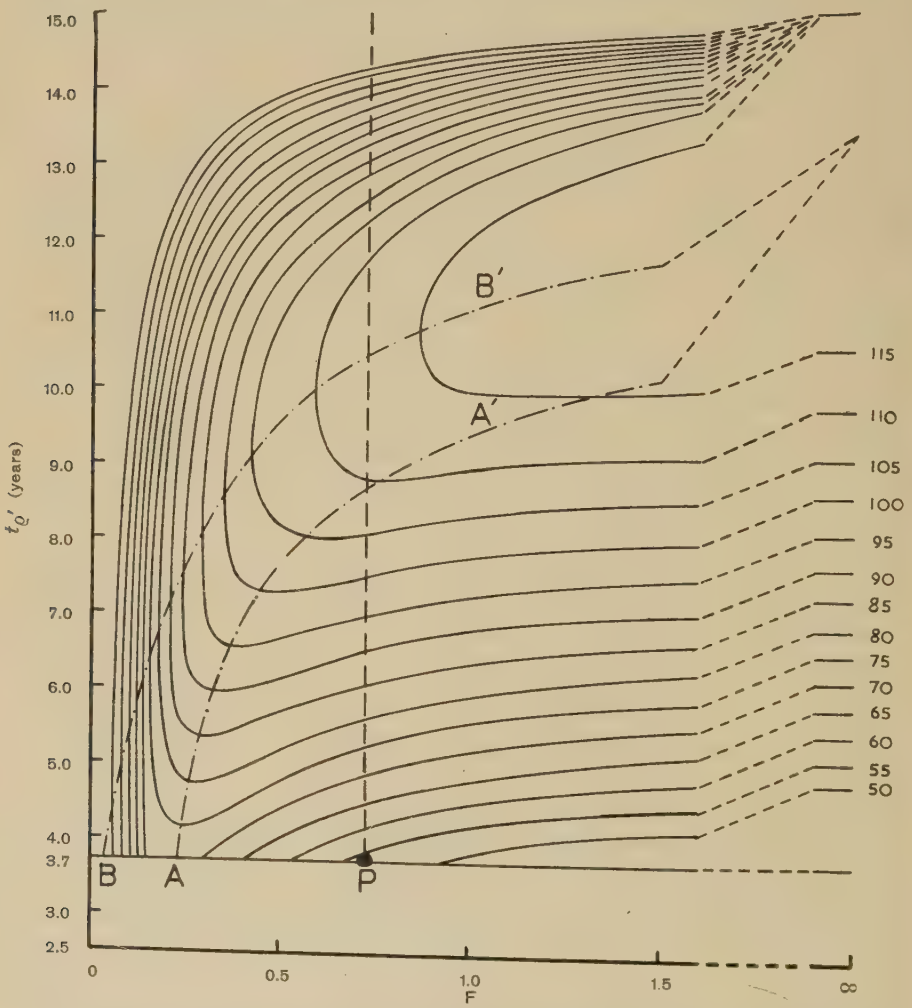

Figure 2. Yield-isopleth diagram for plaice. The yield contours are in units of thousands of tons; the co-ordinates are the fishing mortality coefficient (F), and the age at entry to the exploited phase ($t_{0'}$).

The yield-isopleth diagram and the concept of eumetric fishing.

The characteristics of the fishing activity which may be considered as variables are the fishing intensity and the selective properties of the gear; the latter, in the case of trawl gear, depend largely on the size of mesh in the cod-end. Reference to (4) shows that these characteristics are represented in the model by the fishing mortality coefficient, F, which is proportional to the fishing intensity; and the age $t_{\varrho'}$, at which fish enter the exploited phase, which is a function of the mesh size. Thus there are two independent variables (F and $t_{\varrho'}$) and one dependent variable, i.e., the annual yield, Y_w, and we wish to know how the steady level reached by the latter varies with the particular values of the former which are postulated. This can best be shown by plotting contours of yield with values of F and $t_{\varrho'}$ as co-ordinates. This we have termed a *yield-isopleth diagram* (iso-pleth = equal plenty (Gr.)), and for the plaice it is shown in Figure 2. The horizontal axis shows the scale of F and the vertical axis that of $t_{\varrho'}$ in years. The contours join points of equal yield and are spaced at regular intervals of yield. The diagram does not extend below a value of $t_{\varrho'} = 3{\cdot}7$ years, since this is the estimated average age at which plaice enter the main North Sea fishing area; i.e., it is the age at recruitment t_{ϱ}.

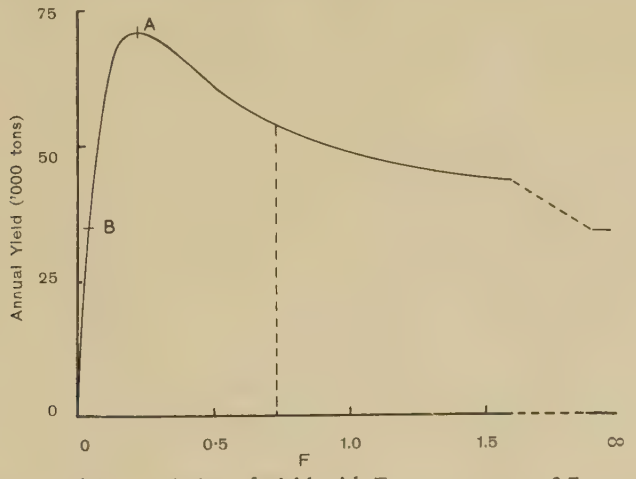

Figure 3. Plaice: variation of yield with F, $t_{\varrho'}$ constant at 3·7 years.

The shape of the more familiar yield-curve in which the mesh size is held constant throughout while the fishing intensity is varied, corresponding to those deduced by B a r a n o v, R i c k e r, and G r a h a m, can be seen from the isopleth diagram by reading horizontally. Thus at a value of $t_{\varrho'}$ of 3·7 years, which corresponds in the plaice to the 70 mm. cod-end mesh in use before the war, it is seen that as F is increased the yield first increases to a maximum at about F = 0·2, and then slowly falls again. The yield along this section is shown in Figure 3, the points A

and B being those crossed by the lines AA′ and BB′ of the isopleth diagram, and the dotted line showing the pre-war level of fishing intensity. However, if a similar section is drawn at a higher value of $t_{\varrho'}$ (e.g., at $t_{\varrho'}$ = 12 years), it will be seen that the yield ascends continuously to an asymptote with increasing fishing intensity. Thus the presence of a maximum in a curve of yield as a function of fishing intensity with the mesh size held constant is not a general feature, but depends on the size of mesh in question. Performing the converse operation on the other hand, namely, tracing the variation of yield with $t_{\varrho'}$ at a constant value of F (i.e., reading vertically), shows that the yield reaches a maximum at some intermediate value of $t_{\varrho'}$ at all except extremely small values of F. A vertical section at the pre-war value of F = 0·73 is shown in Figure 4, the points A and B having the same significance as before.

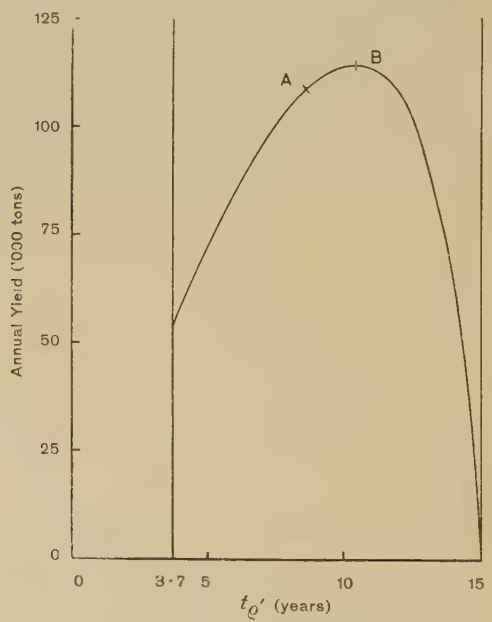

Figure 4. Plaice: variation of yield with $t_{\varrho'}$, F constant at 0·73.

The point on the isopleth diagram corresponding to the pre-war fishing intensity and cod-end mesh size is shown by the solid circle at F = 0·73, $t_{\varrho'}$ = 3·7, and it is thus seen that there exists a wide range of combination of fishing intensities and mesh sizes which could have produced a greater yield. This is the first practical lesson of our enquiry — that precise formulation of the problem for the North Sea plaice confirms what so many of the Council's deliberations have frequently stated, namely, that there is ample room for improvement in the plaice fishery, either by increase of mesh-size or by alteration of the fishing intensity, or by a combination of both measures.

The properties of the yield-isopleth diagram can, however, lead us further, and indicate the principle according to which adjustment of these two factors should be made to produce the best results. It is evident from Figure 2 that by taking a number of vertical sections at different values of F a family of curves could be obtained, of which the curve of Figure 4 is a member. In each of these curves the yield reaches a maximum at a certain value of $t_{\varrho'}$, and hence at a certain mesh size, depending on the value of F in question. These maxima are joined in Figure 2 by the line BB′, which we propose to call the *eumetric fishing curve* (eu-metros = well-balanced, (Gr.)) because for any fishing intensity it defines the mesh size which will enable the greatest yield to be obtained at that intensity.

We suggest that the adjustment of fishing intensity and the age at which fish enter the exploited phase according to this criterion of eumetric fishing is the principle that should underlie the regulation of any commercial fishery in which the characteristics of the fish population and of the gear are such that the value of $t_{\varrho'}$ can be varied. Thus it is applicable not only to the North Sea plaice but to the demersal fisheries of the North Sea in general, in so far as is compatible with the practical considerations which must be taken into account when framing actual regulative measures. It must be mentioned that the complementary nature of fishing intensity and the age at which fish first enter the exploited phase as a principle of fishery regulation has also been appreciated by Nesbit (1943), Ricker (1945), and Baerends (1947).

With the help of this concept of eumetric fishing a generalized relationship between yield and fishing intensity can be established, which is of special relevance to our problem of determining the best steady state at which a fishery should operate. In this yield-curve the selective properties of the gear are varied simultaneously with the fishing intensity in accordance with the requirements for eumetric fishing as defined above, instead of remaining constant throughout as in the yield-curve of Figure 3. This we shall call the *eumetric yield curve*. Its shape can be seen roughly from Figure 2 by following the line BB′ as it crosses the yield contours, but it is best shown two-dimensionally by plotting yield against F as in Figure 5 (curve P_1), remembering that the value of $t_{\varrho'}$ is implicitly adjusted throughout to match the change of F according to the eumetric fishing curve BB′. There are, of course, certain fisheries where the age at entry to the exploited phase is determined largely or completely by the biological characteristics of the fish population, an extreme example being the Fraser River fishery for Pacific salmon. In such cases it is necessary to base regulation on a yield curve in which $t_{\varrho'}$ cannot take the full range needed for eumetric fishing, or even is constant throughout, as in Figure 3, but the discussion of fishery economics and the determination of the optimum fishing intensity given below are still applicable.

The important feature of the eumetric yield curve P_1 of Figure 5 is

that it has no maximum but ascends continuously to an asymptote as the fishing intensity is increased. Although this curve is based on the plaice and has been calculated from the simple model with constant parameters, all the investigations we have made so far suggest that this is a very general characteristic of eumetric yield curves for one species alone. For example, the eumetric yield curve for haddock calculated with constant parameters is shown by curve H_1 of Figure 5; while incorporating into the model the relationships between growth and population density which have been found in the plaice and haddock merely lowers all points on the curves P_1 and H_1, giving the results shown by curves P_2 and H_2. A similar effect is produced by a density-dependent natural mortality rate; but when the number of recruits is

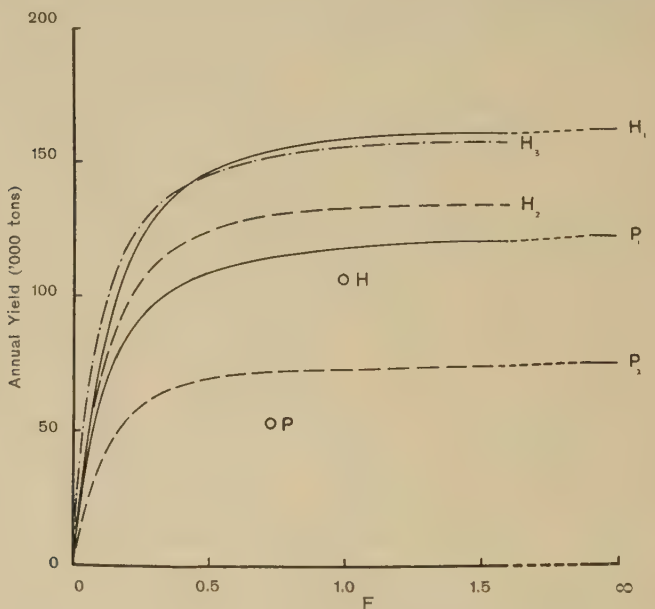

Figure 5. Eumetric yield curves for plaice (P) and haddock (H).

made to depend on the egg-production of the parent population, and hence to vary with density, the tendency is to raise the level of the eumetric yield curve. Now, in reality, both growth and recruitment may be expected to vary simultaneously with density, and if this combined dependence is incorporated in the theoretical model the resultant effect may well lead to a eumetric yield-curve which does not differ greatly from that calculated with constant parameters. An example based on the haddock which illustrates this point is shown in Figure 5 by curve H_3. It must be emphasized that insufficient is known at the present time to determine the actual relationship between recruitment and population density in either the haddock or plaice with precision, and although that used to construct curve H_3 is not inconsistent with the available data, the true curve may be somewhat below or above

curve H_1. Nevertheless, the finding that is significant in the present connexion is that curve H_3 is still of the same general shape as the other curves shown in Figure 5. The importance lies in the fact that this curve embodies simultaneously the two criteria which have long been realized as forming the biological basis of fishery management, namely, on the one hand, of obtaining the best balance between growth and mortality, and on the other, of maintaining recruitment at the most effective level.

The points P and H of Figure 5 show the average European yields of plaice and haddock which were obtained annually from the North Sea during the appropriate pre-war periods. Each lies below the corresponding eumetric yield curves because in neither case was the fishing eumetric; specifically, the fishing intensity was too high for the mesh in use.

The concept of eumetric fishing can also be applied to a fishery based on two or more species of fish of commercial importance which are caught simultaneously by the same gear, as is the case in the North Sea. Thus for any given fishing intensity there is a mesh size which enables the greatest combined yield to be obtained, although this combination of fishing intensity and mesh size might not be eumetric for any one of those species alone.

Fishery economics and the concept of optimum fishing.

We have shown how the properties of our theoretical model can lead to the concept of eumetric fishing and the construction of a eumetric yield curve. It is now worth considering briefly whether any generalized statement can be made concerning the position on the eumetric yield curve at which a fishery should operate to obtain the best results.

The problem is essentially an economic one, to be reckoned in terms of the value of the yield and the cost of obtaining it. Clearly, it is not desirable to attempt to obtain the greatest possible yield, since owing to the shape of the eumetric yield curve this can be achieved only with an extremely high fishing intensity, and hence at a prohibitive cost. On the other hand, if too low a fishing intensity is used, even though the fishing is eumetric, the yield will be unnecessarily small, and a relatively small increase in intensity would enable a greater yield to be obtained without as large an increase in the cost of fishing (see, e.g., Huntsman, 1951).

To take the analysis further, it is necessary to convert the scales of yield and fishing intensity of the eumetric yield curve into the economic equivalents of the total value of the annual yield and the total running costs of generating any given fishing intensity. This is perhaps the central problem of fishery economics and it is not a simple one; for our present purposes we need not attempt to establish the detailed form that these relationships will take, and it is sufficient to state that the value of the yield will increase continuously as its weight increases, and that the running costs will similarly increase as the fishing intensity increases. Thus the value-cost curve will be of the same general shape as the

eumetric yield curve of which it is the derivative, a hypothetical example being shown by curve (a), Figure 6. In a fishery based on a number of different species a combined value-cost curve could be constructed in a similar way, with the contribution of each species weighted according to its price, i.e., its value per unit weight.

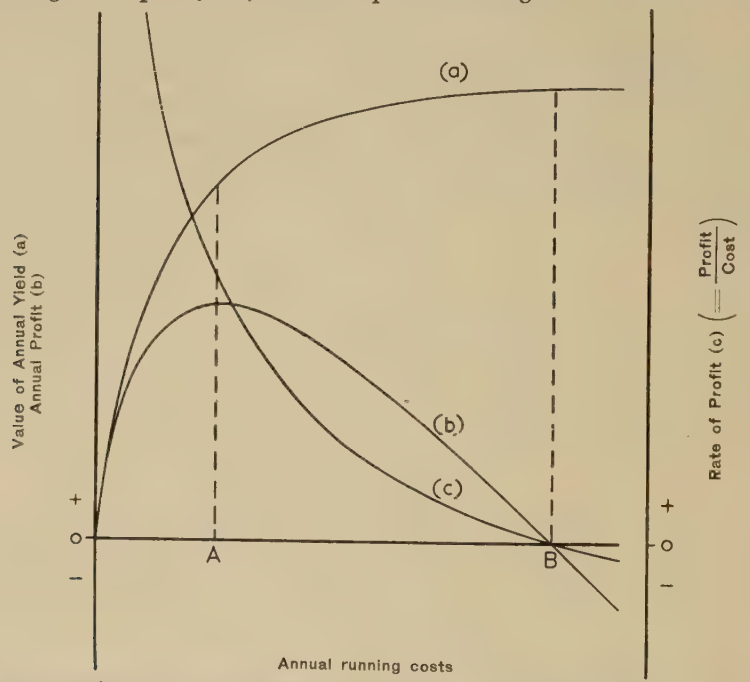

Figure 6. Hypothetical curves of value (a), profit (b), and rate of profit (c), as functions of running costs. The vertical dotted lines show the points on the value-cost curve corresponding to maximum profit (A) and zero profit (B).

The *annual profit* to the industry at any given fishing intensity can now be assessed as the difference between the total value of the yield and the total running costs at that intensity, the profit curve derived from curve (a) being shown by curve (b). This will always reach a maximum at a certain level of fishing intensity, and become zero at the intensity where the running costs are equal to the value of the catch. The *rate of profit*, i.e., the profit as a percentage of the cost, is shown by curve (c); it decreases throughout the range of increasing fishing intensity.

On economic grounds alone, and supposing that the fishing industry is to be regarded as a self-supporting economic unit, the fishing intensity which enables a good balance to be achieved between the benefits to the industry and to the consumer is perhaps that corresponding to the maximum profit level, i.e., the maximum of curve (b). There will be other factors, however, social or political, which may make it desirable for a somewhat higher fishing intensity to be exerted, and hence a little

greater yield to be obtained, though this intensity is unlikely to be much higher owing to the decrease in return for outlay that would result. At some level of fishing intensity there will, nevertheless, be the best compromise between all these factors, and we propose to call this the *optimum fishing intensity*. Our use of this term to refer to the best balance between economic, social, and political factors is similar to that of Sette (1943), but this author does not include the criterion of eumetric fishing in his definition.

To summarize, we have shown that study of the biological properties of a fish population can lead only as far as the determination of eumetric fishing and eumetric yield curves for that fishery. The point on the eumetric yield curve at which it is best for the fishery to operate — the optimum fishing intensity — does not correspond to a maximum yield nor is it determined by any particular biological criterion, but must be decided purely with reference to economic factors and administrative policy.

Conclusions for the North Sea demersal fisheries.

We introduced our problem by mentioning that the history of the North Sea demersal fisheries during the past fifty years has shown that although a steady state has been reached in the absence of regulation, the indications are that this was not the best that could be achieved. Our investigations into the properties of theoretical models of an exploited fish population, using the plaice and haddock for purposes of illustration, have confirmed this conclusion and shown why the balance reached between the two wars did not enable the productivity of these two stocks to be used to the best advantage. The conclusion that regulation is essential to enable the best results to be obtained is inescapable, and we suggest that the concepts of eumetric and optimum fishing put forward above can establish the objective which regulation should ultimately achieve, even though the practical difficulties arising in regulating a complex area such as the North Sea may mean that what is "best" for the area as a whole has to be something of a compromise. The basic parameters whose values must be adjusted by regulative measures to obtain eumetric and optimum fishing are the fishing mortality coefficient, F, and the age, $t_{\varrho'}$, at which fish enter the exploited phase. Thus any measure which changes the fishing intensity or the selective properties of the gear can be effective, though the more direct and predictable its effect the better.

Although it is not possible at the present time to estimate with accuracy the requirements for optimum fishing of the North Sea as a whole, all our investigations lead to the conclusion that the fishing intensity will need to be considerably lower than it was before the war, and that some increase in mesh size will be necessary, though the possibilities of the latter are more limited owing to the presence of small but relatively valuable fish such as sole. But our inability to define precisely the requirements for optimum fishing does not mean that less

ambitious regulation could not be undertaken with advantage. In any case, the attainment of optimum fishing of the North Sea cannot be expected rapidly in a single step, if only because of the social and economic readjustments which a permanent and large reduction in fishing intensity would involve. The changes in fishing intensity and mesh size proposed at the 1947 Overfishing Conference are practicable first steps in regulation of the North Sea demersal fisheries; or as Graham (1951) has emphasized, even stabilizing the fishing intensity at the present level would at least enable some economic benefit to be obtained from new inventions and technical advances in fishing methods, whereas with unregulated fishing their effects would be harmful. The approach to optimum fishing is perhaps best visualized as proceeding in a series of steps, with our understanding of the fisheries and our knowledge of where the optimum lies advancing simultaneously.

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A Note on Market Sampling of Halibut.

By

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A full understanding of the fluctuations in any fishery depends on knowledge of the age composition of the stocks. In spite of the importance of the halibut fishery in western Europe there are few published data on the age composition of halibut stocks. The lack of information is due chiefly to the difficulty of obtaining material, and there are several reasons for this. The halibut is taken usually on lines, and since our research vessels concentrate for the most part on trawling, they can provide very little material. It is thus necessary to resort to market sampling. However, this is rendered difficult since otoliths are required for age-determination, scales being unsatisfactory for this purpose in halibut. Two methods of market sampling for halibut have been in use for some time at Aberdeen, and since these combined provide data on all sizes of halibut, it is thought that the following details would be of interest to other workers.

When dealing with trawlers' catches, measurement data alone are required. The catches consist almost entirely of two- and three-year-old fish, and there is very little overlap between the size ranges of each age-group. Figure 1 shows the length distribution of 1114 halibut landed by

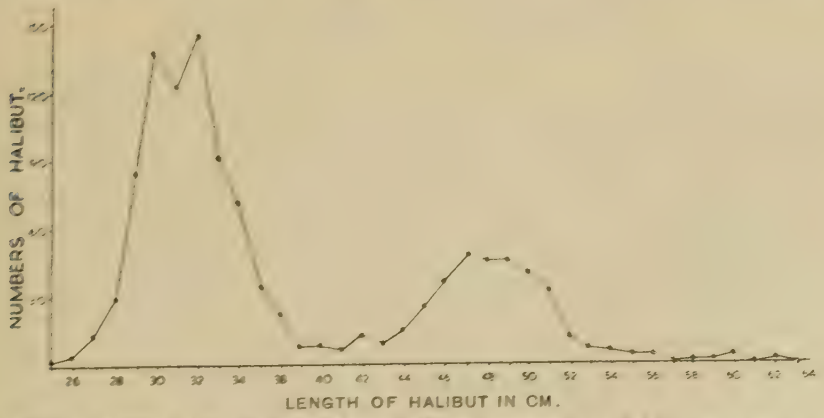

Figure 1. Length distribution of Faroe halibut from catches of Aberdeen trawlers. 5.—15. May 1952.

trawlers at Aberdeen between 5. and 15. May 1952. In utilizing data collected on research vessels, and by occasionally buying a few fish at the market to secure otoliths, it is possible to determine the proportions of two- or three-year-old fish lying within the overlap (in Figure 1, 38—40 cm.) and also to find the upper limit of the range of three-year-old fish. It is thus possible to calculate the mean size of these two age-groups, and the inaccuracy, due to the slight overlap, affects only the second decimal place.

Sampling from liners' catches presents a different problem. Since only large halibut are involved it is necessary to secure otoliths. The heads of large halibut are nearly always removed by fish merchants and kept in barrels pending delivery to fishmeal factories. It was found that in approximately 65 % of the fish, the otoliths are retained in the head, and by visiting several fish yards it is thus possible to make a good collection of otoliths.

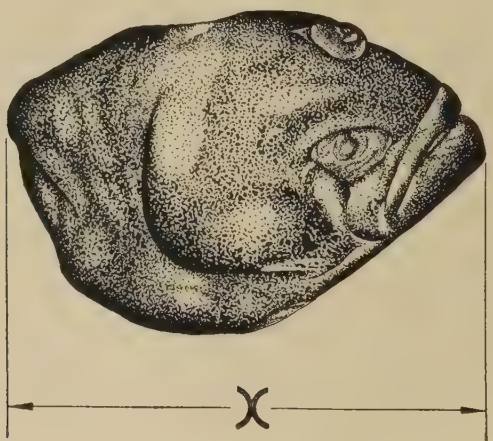

Figure 2. Showing the measurement "*x*" used in the formula connecting head length and total length of halibut.

This method of collection involves several difficulties. If the otoliths collected are to represent a random sample from the halibut catch of one ship, it is necessary to ensure that the fish merchants visited have bought fish from only one vessel, that they have made no size selection when buying at the market, and that they have headed all fish bought.

Unless the worker is present when the head is being removed, he has no knowledge of the length of fish from which the otolith was taken. It was therefore necessary to derive a factor which would enable some measurement made on the separate heads to be converted to total lengths of fish. The measurement used was the length from the tip of the snout to the most posterior part of the operculum (see Figure 2). Due to the curvature of the head and to the fact that the snout and operculum tip are not directly opposed, it is sometimes difficult to make

an accurate measurement. A simple measuring device has therefore been constructed (see photograph, Figure 3).

In determining the factor, the head lengths (as defined above) and total lengths of 312 fish from west Iceland were measured, and the following regression line was derived:—

$$Y = 3{\cdot}83x + 7{\cdot}79$$

where Y = total length of fish, x = length of head.

Using this formula, the total length of a fish can be calculated from the separate head. The measurements on which the formula is based were made on fish between 50 cm. and 200 cm., and while it is probably

Figure 3. The method of measuring halibut heads.

safe to apply it to fish above the upper limit of this range, it may not be advisable to use it for very young fish. However, for these young fish the first method above is applicable. When collecting the data no distinction was made between male and female fish, but the small range of total lengths equivalent to any given head length suggests that sexual difference is not significant.

Finally, these figures apply only to fish from west Iceland but measurements made from North Sea material suggest a rather similar regression line. However, when any new area is studied, the regression should be checked.

By means of these two methods it is possible to utilize commercial catches to carry out age analyses of halibut stocks.

Sur l'Etat de Maturité Sexuelle d'un Germon pris en Mer Tyrrhénienne.[1])

Par

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Ovaires et oeufs du germon.

B a c k et L e g e n d r e (1932) ont étudié "L'état sexuel du Germon pendant la saison de pêche", par l'examen des ovaires prélevés, à Concarneau, au moment où le poisson est vidé, aussitôt après son arrivée sur le pont, et immédiatement placés dans l'eau de mer formolée.

D'après ces auteurs, les ovaires formaient des cordons oblongs dont les dimensions (longueur, largeur, épaisseur), prises sur trois individus, étaient les suivantes: 1) 120×18×6—7 mm. (fin Juillet); 2) 143×19·5—13·5 mm. (début de Septembre); 3) 160×19×14 mm. (début d'Octobre).

L'examen histologique de ces germons de l'Atlantique a montré, sur des coupes transversales, des ovules ayant: 1) de 40 à 88 μ (fin Juillet); 2) de 60 à 90 μ (début de Septembre); 3) 70 à 100 μ (début d'Octobre).

En ce qui concerne le germon de la Méditerranée (Mer Tyrrhénienne), pêché au début du mois de Juillet, les dimensions (longueur et largeur) des ovaires étaient: à droite, 260×30 mm. (poids 75 g.); à gauche, 220×30 mm. (poids 65 g.).

Il est donc manifeste que ces ovaires sont beaucoup plus développés que ceux des germons de l'Atlantique ci-dessus mentionnés, quelle que soit l'époque considérée, un excédant de 100 mm. en longueur et 10 mm. en largeur étant vérifié (vraisemblablement correspondant au double du volume) par rapport aux ovaires d'Octobre.

L'examen histologique — après fixation, inclusion, coupage, coloration et montage — a montré de nombreux "oeufs mûrs" (ou presque mûrs), dont la majorité mesurait de 310 à 400 μ, quelques follicules vidés en voie de comblement, ainsi que des oocytes à la troisième période

[1]) Campagne du navire océanographique "Président Théodore Tissier".

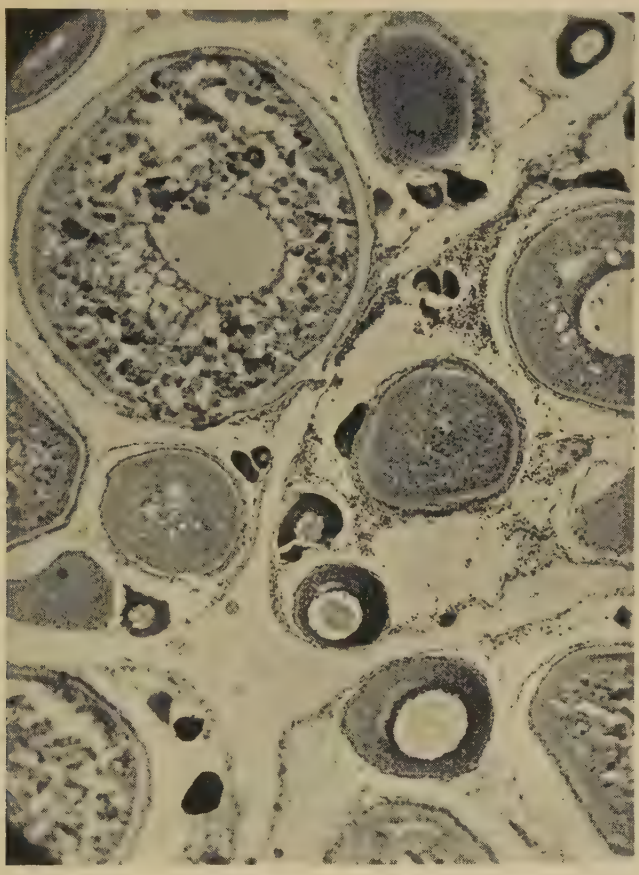

Figure 1. Coupe de l'ovaire d'un germon pris en Mer Tyrrhénienne le 4 Juillet 1950.

d'activité (à anneau dit de croissance) et à des phases moins avancées (Figure 1).

Il s'agit donc d'un stade à peu près égal à celui que nous avons (F r a d e, 1937) désigné, pour le thon rouge, par la lettre B, les vestiges d'un commencement de ponte fractionnée étant dénoncés par de grands espaces entre les oocytes, accompagnés d'une relative abondance du tissu conjonctif de comblement. Ajoutons, en outre, que les dimensions ci-dessus enregistrées, pour les "oeufs mûrs", sont à peu près celles que nous trouvons chez les ovaires du thon rouge, au même stade de la maturité, et trois à quatre fois celles qu'ont indiqués B a c k et L e g e n d r e, pour le germon atlantique, au mois d'Octobre.

Ce résultat semble être, de premier abord, en opposition à ce qui a été observé, en Méditerranée, par S e l l a (1924) et par S a n z o (1925), dans les eaux du détroit de Messine, c'est-à-dire, l'existence d'oeufs et de larves pendant le mois d'Août. Ce dernier auteur y a trouvé, dès le début d'Août, des oeufs fécondés, sphériques, transparents, à gouttelette

huileuse, de 0·84 à 0·96 mm. de diamètre, lesquels, après deux jours, donnent sortie à une très petite larve de 2·5 mm.

Navarrete (1898) supposait que la reproduction du germon avait lieu en automne.

Mais il faut toutefois remarquer que notre observation est forcément limitée à un seul individu, et que l'on ignore donc s'il est en réalité assez représentatif de l'état sexuel de l'ensemble des germons méditerranéens, à l'époque où il a été capturé.

Périodes et lieux de frai, en Méditerranée et en Atlantique.

Pour le thon rouge, il est connu (Scordia, 1934; Frade, 1937) qu'en Méditerranée il n'y a pas toujours un synchronisme parfait de la maturité sexuelle, chez les divers groupes de thons fréquentant cette mer, dans une même année et d'une année à l'autre (1932 et 1933). D'après Scordia, l'émission des produits génitaux a été plus avancé en 1933 que l'année précédente, puisque les premiers thons rouges génétiques capturés sur la côte sicilienne du détroit de Messine (23 et 28 Juin) avaient déjà émis en partie les produits génitaux, tandis qu'en 1932, tous les thons capturés du 18 Juin au 4 Juillet avaient les gonades pleines et turgides, le videment n'ayant commencé qu'à partir de cette dernière date; cependant, au mois de Mai 1933, deux individus du sexe femelle, capturés le 20 et 21, à l'embouchure du détroit de la Mer Tyrrhénienne, avaient déjà les gonades pleines et turgides.

A notre tour, ayant fait, en 1933, l'examen histologique de quelques gonades de thon rouge méditerranéen, dont quelques échantillons nous ont été parvenus par M. Heldt, nous avons reconnu que les thons capturés le 20 Juin dans les thonnaires de Sidi-Daoud étaient au même stade de la maturité sexuelle (♂ au stade A; ♀ aux stades B et C), que les thons pêchés vers le commencement de la saison, le 4 Juin, au Cap Zébib, et partant manifestement en retard par rapport à ces derniers et à ceux provenant de Monastir, le 15 Juin (♂ au stade B; ♀ au stade CD). Donc un synchronisme n'a pu être vérifié.

Il semble plutôt que les thons forment des groupes iso-génétiques, chacun constitué par des individus, mâles et femelles, à peu près au même stade de la maturité sexuelle, se déplaçant, indépendemment, vers les lieux de ponte.

Nous n'avons pas maintenant des éléments pour en faire des comparaisons, en ce qui concerne le germon, mais il est vraisemblable que des faits pareils puissent être vérifiés dans l'avenir.

La capture d'une femelle de germon oeuvée au commencement du mois de Juillet, en Méditerranée, ne semble donc pas constituer un fait exceptionnel; tout au contraire, il rentre dans le cercle de ce qui a été observé pour le thon rouge.

Mais ce fait, si banal soit-il, vient cependant attirer l'attention des biologistes, une fois de plus, pour les différences, peut-être raciales, trouvées des deux côtés du détroit de Gibraltar: dans l'Atlantique, ainsi que Back et Legendre l'ont relevé, depuis la fin Juillet jusqu'au

mois d'Octobre, les oocytes sont en période de croissance, très lente; tandis que, dans la Méditerranée, ils sont mûrs ou presque mûrs dès le commencement du mois de Juillet jusque pendant le mois d'Août. On est donc autorisé à supposer, avec le Danois (1921) que, dans l'Atlantique, la reproduction est terminée avant le début de la pêche, c'est-à-dire, avant l'arrivé à la côte ibérique, en Avril-Mai.

Selon le Danois (1921—1922), Belloc (1927) et le Gall (1949), le germon atlantique, tous les ans, se rend vers le nord, avec les eaux transgressives, chaudes (à plus de 14° C.) et salées, jusque dans le golfe de Gascogne, l'entrée de la mer de l'Irlande et le plateau continental celte, c'est-à-dire, jusqu'à la limite de ces eaux, où il trouve une nourriture abondante (sardines, maquereaux, harengs, anchois, etc.), y étant l'objet d'une pêche intense, de même qu'aux environs de la côte ibérique pendant les mois de Juillet, Août, Septembre et début d'Octobre. À la fin de la saison, retournant vers le sud, lors de la régression des eaux, il quitte les côtes ibériques, et se rend vraisemblablement, cette fois, vers les Açores et Madère, où le germon ("Atum-voador") est pêché pendant l'hiver.

Il semble donc tout naturel d'entreprendre des recherches répétées dans cette zone de l'Atlantique et encore plus au sud, ainsi que dans la Méditerranée, ce que la croisière du "Président Théodore Tissier" vient d'annoncer.

En effet, toutes les données acquises, au sujet de la ponte des thonnidés, renseignent que les aires respectives sont, pour la plupart, très éloignées des côtes. C'est le cas des larves trouvées en Méditerranée (Sella, 1924; Sanzo, 1925), dans l'Atlantique (Lütken, 1880; Ehrenbaum, 1924), et dans le Pacifique (*vid.* Schaeffer, 1948).

Il est aussi souhaitable que la coopération internationale, préconisée aux "Conférences du Thon", à Malaga et à Salammbô (1949), devienne une réalité, pour la recherche des frayères des Thonnidés, ces poissons qui, selon les mots de Schaeffer (1948) "... constitute an international resource. They call no country home; they pass the greater part of their lives and reproduce their kind outside the territorial limits of any nation".

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A Device for the Quick and Accurate Measurement of Carapace Length in Prawns and Shrimps.

By

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Introduction.

The length of the carapace from the base of the eye notch to the posterior mid-dorsal edge has been adopted as the standard measurement in many studies of prawns and shrimps. The use of this measurement has many advantages over the measurement of total length, from the tip of the rostrum to the posterior edge of the telson, since in preserved samples of crustacea the abdomen is very frequently flexed, while not uncommonly the rostrum is damaged.

The carapace measurement needs to be made accurately to within 0·25 mm., and since samples of prawns and shrimps must necessarily be large to give intelligible frequency-distribution curves, a device is needed which allows of rapid measurement without loss of accuracy. It is considered that the instrument in use at the Conway and Burnham-on-Crouch research laboratories fulfils these requirements.

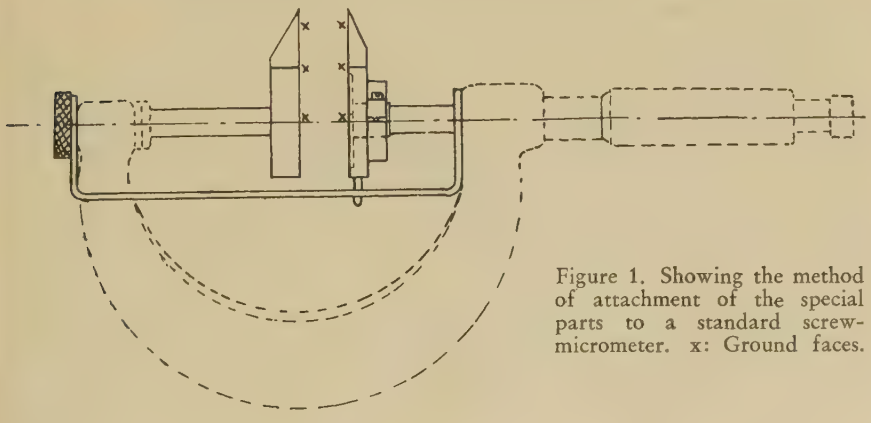

Figure 1. Showing the method of attachment of the special parts to a standard screw-micrometer. x: Ground faces.

Description of the instrument.

The instrument is essentially a screw-micrometer fitted with special jaws, each provided with a point about 2·5 cm. long projecting at right

angles to the main axis of the micrometer. The internal surfaces of these points are held automatically in line with the faces of the micrometer, and parallel, so that at any moment the distance between the inside opposed surfaces of the points is the same as that shown on the micrometer scale. How this is effected is shown in Figures 1 and 2.

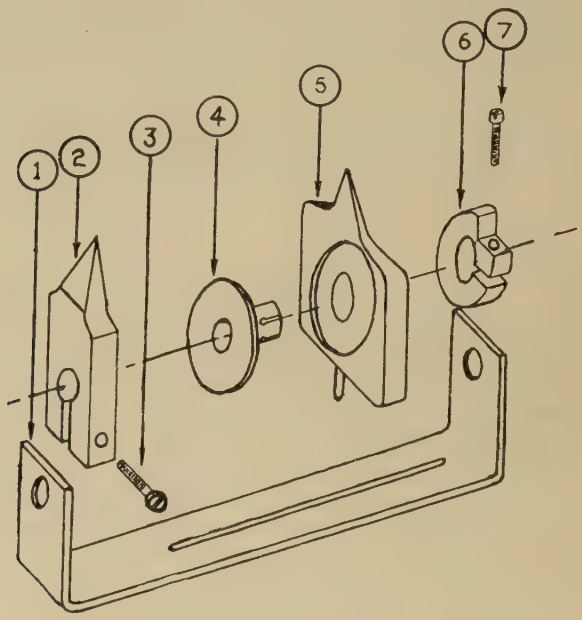

Figure 2. Exploded diagram showing the special parts used. 1. Guide plate; 2. Anvil stop; 3. Locking screw; 4. Locating collar; 5. Movable stop; 6. Clamping collar; 7. Locking screw.

To the fixed face of the micrometer (or anvil) there is clamped a point projecting at right angles in such a position that the face of the point is flush with the end of the anvil. To the movable face of the micrometer is fixed a point of similar size and shape held in place by two collars. The collars and micrometer spindle rotate freely inside the body of the floating point, which is held parallel to the fixed point by a pin projecting in the opposite direction to the point and confined within a slit cut in a brass guide. The whole micrometer is clamped in a jointed wooden stand with a hardwood base in such a position that the spindle is horizontal and projects to the right. The joint allows the micrometer to be raised and lowered in the stand. In practice the most convenient height for rapid measurement is such that the left hand holding the prawn or shrimp by the antennae and antennal scales rests on the base-board (Figure 3). The fixed point of the micrometer is inserted in the eye notch and with the right hand the micrometer is screwed up until the inner surface of the floating point touches the

hinder edge of the carapace in the mid-dorsal line. The distance between the points is read off directly from the micrometer scale. We are measuring *Crangon, Pandalus,* and *Leander* to 0·2 mm. Repeated measurements of the same individual rarely vary by more than 0·1 mm. with this instrument.

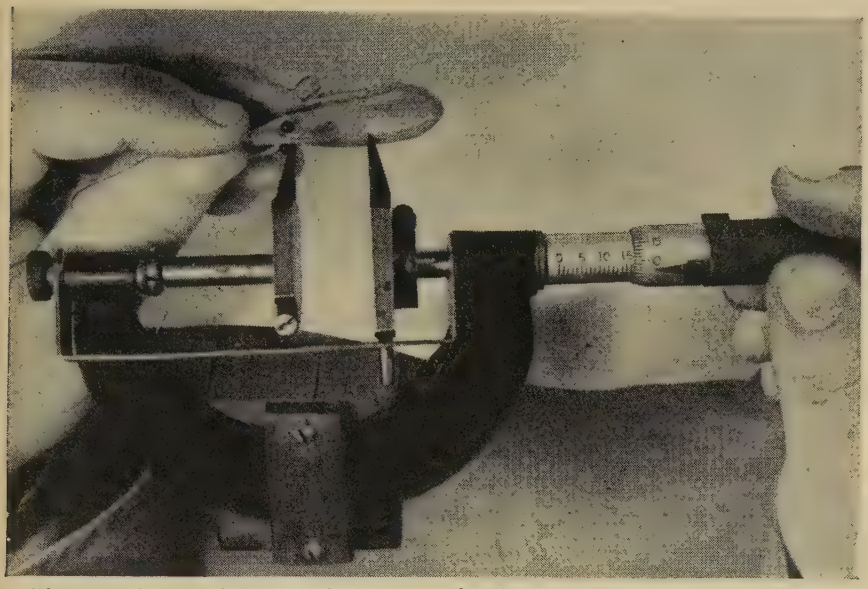

Figure 3. Screw-micrometer device in use for the measurement of carapace length in *Pandalus montagui.*

With an assistant to write down the data we find that *Crangon vulgaris, Leander serratus,* and *L. squilla* may be measured and sexed at the rate of 200 to 250 per hour. *Pandalus montagui* may be measured just as quickly, but sexing requires the use of a binocular microscope. No difficulty has been experienced in measuring juvenile prawns and shrimps down to a carapace length of 4—5 mm.; below this size it is not easy to hold the small individuals without obtruding the thumb in the way of the point to be placed in the eye notch.

The standard type of 5 cm. micrometer, with fixed anvils of two lengths, giving measurements between 0·0 and 2·5 cm., and 2·5 and 5·0 cm., will suffice for the measurement of all European species of prawns and shrimps.

In the development of this instrument we have received much assistance from Mr. Morris Jones, who also drew the sketches from which Figures 1 and 2 were prepared.

Contribution à l'Etude de *Mytilus edulis* L. parasité par *Mytilicola intestinalis* Steuer.

Par

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Laboratoire d'Anatomie et d'Histologie
Comparées de la Sorbonne.

L'invasion récente des eaux zélandaises par *Mytilicola intestinalis* et les graves parasitoses qui se sont déclarées chez *Mytilus edulis* ont posé le problème du mécanisme des troubles déclenchés par la présence de *Mytilicola* dans l'intestin de son hôte. Meyer et Mann (1951), ont mis en évidence chez ce dernier un abaissement sensible du poids sec sous l'influence d'une diminution du pouvoir filtrant et d'une augmentation des échanges respiratoires. L'étude histologique et histochimique de moules parasitées m'a permis d'apporter les précisions suivantes sur les rapports de *Mytilicola* et de son hôte et sur les principales modifications qui surviennent chez celui-ci.

Que ce soit chez *Mytilus galloprovincialis* Lamk. ou bien chez *Mytilus edulis* L., *Mytilicola* siège en général dans le tube digestif. Korringa (1950) signale sa présence dans les conduits de la glande digestive, je l'ai parfois rencontré dans les vaisseaux sanguins (aorte et vaisseaux branchiaux) et dans le tissu conjonctif, dans ce dernier cas il paraissait enkysté par les phagocytes.

Il est d'observation courante qu'à ses divers stades parasites *Mytilicola* conserve la faculté de se déplacer par des mouvements reptatoires. Heldt (1951) indique qu'il se trouve fixé dans l'intestin par ses antennes, la tête tournée vers l'extrémité antérieure de son hôte; il semble en effet s'orienter en sens inverse de la circulation du bol alimentaire. L'examen histologique de moules fixées sur le lieu de leur capture montre que *Mytilicola* peut se rencontrer dans tout le tube digestif depuis l'estomac jusqu'au rectum, mais qu'il est surtout abondant dans l'anse formée par la partie la plus antérieure de l'intestin moyen. Il

peut distendre énormément la portion du tube digestif qui le contient (2·5 mm. de diamètre au lieu de 1·3 mm. pour le rectum d'un individu au niveau où il abritait huit parasites à la fois).

On connaît de nombreux exemples de Mollusques parasités par des Crustacés Copépodes, ceux-ci doivent être considérés comme des parasites endémiques (Dollfus, 1951) et ne causent à leurs hôtes aucun dommage apparent. Mais, si leur nombre vient à s'élever, la mortalité des Mollusques parasités augmente dans de larges proportions Odlaug, 1946). Chez *Mytilus edulis* parasité par *Mytilicola,* Korringa et Lambert (1951), Meyer et Mann (1951), soulignent que le nombre de trois parasites n'affecte pas l'état de la moule et que la mortalité ou des troubles physiologiques ne se manifestent qu'à partir de dix parasites au moins. On ne peut donc s'attendre, sur le plan d'une étude histologique et histochimique, à des résultats concluants que si l'on s'adresse à des exemplaires très gravement parasités. Aussi ai-je choisi pour cette étude des individus venant de bancs où *Mytilicola* sévit tout particulièrement (Brest et divers bancs zélandais). Après une comparaison avec des moules totalement exemptes de parasites, j'ai adopté comme témoins les Mollusques les moins parasités, de même provenance que ceux qui font l'object de ce travail. Ainsi ont été exclues les différences provenant simplement des facteurs écologiques.

Modifications des réserves chez les individus parasités.

L'importance des réserves de glycogène accumulées par les Mollusques Lamellibranches est un fait bien connu. Chez la moule, ces réserves sont localisées pour la plus grande part dans le tissu conjonctif (exception faite des réserves des muscles et du pied). Un des effets les plus directs de la présence de *Mytilicola* dans l'intestin de la moule est de toucher, électivement parmi les substances de réserve, les réserves de glycogène[1]). Chez les moules gravement infestées, les cellules de Leydig du tissu conjonctif paraissent privées de glycogène, alors que les parasites en présentent de grandes quantités, dans des cellules de même type que les cellules de Leydig des Mollusques. La structure du tissu conjonctif de la moule peut d'ailleurs se modifier dans les cas où le parasitisme est très accusé; l'aspect de parenchyme qu'il revêt normalement fait place à une structure en réseau où prédominent les "cellules fixes". Ces structures sont comparables à celles que l'on peut observer chez des huîtres ayant perdu la quasi-totalité de leurs réserves de glycogène au cours d'un jeûne rigoreux (Couteaux-Bargeton, 1946).

Les réserves de glycogène que contient l'épithélium de l'intestin direct et de l'intestin récurrent, peu importantes d'ailleurs dans l'économie générale, ne semblent diminuer que chez les moules les plus atteintes. L'état d'inanition, plus peut-être que des troubles de l'assimilation, suffirait à expliquer ce phénomène.

[1]) Ce phénomène est particulièrement facile à mettre en évidence à l'époque de l'année où a été effectuée cette étude (Février—Mars). La moule en bon état physiologique présente alors une grande quantité de réserves qui disparaîtront au cours de la gamétogenèse (Daniel, 1921—1922).

Les dosages de Meyer et de Mann (1951), indiquent une légère diminution du taux des réserves de graisses, la disparition des cellules de Leydig qui en contiennent un peu, pourrait en rendre compte.

Modifications de la glande digestive.

Indépendamment de la réduction du volume de la glande digestive et du nombre de ses tubules, on distingue au niveau de la plupart d'entre eux les modifications de structure suivantes: l'épithélium de revêtement des tubules a perdu son aspect caractéristique dû à l'alternance des groupes formés par les hautes cellules fonctionnelles et par les petites cellules d'attente; il se compose de petites cellules de taille uniforme (14 μ de hauteur). La lumière limitée par ces tubules paraît de ce fait très accrue et, par suite de la disparition des saillies dessinées par les groupes de cellules fonctionnelles, de section ovale ou arrondie.

L'étude histochimique de ces épithélium ne permet pas de mettre en évidence de différences notables entre ses cellules. Celles-ci présentent au sein d'un cytoplasme dont la basophilie semble s'expliquer par une certaine abondance de ribose-nucléo-protéines, de volumineuses granulations groupées autour du noyau à l'opposé du pôle libre de la cellule. Ces granulations qui possèdent certaines des affinités colorantes des grains de sécrétion, se colorent en rouge par la réaction de Hotchkiss et peuvent être considérées comme des glycoprotéines (Catchpole, 1947). La même réaction colore également dans la lumière des tubules une substance amorphe condensée parfois en gouttelettes; cette substance est encore mise en évidence par le bleu de toluidine et l'hématoxyline de Gomori.

A côté des tubules ainsi modifiés et qui rappellent, par leur structure au moins, les transformations entraînées dans la glande digestive par un jeûne expérimental (Mansour et Zaki, 1947), on observe une faible proportion de tubules où l'épithélium de revêtement a conservé son aspect normal. On peut d'ailleurs caractériser dans ses hautes cellules fonctionnelles de volumineuses granulations particulièrement nombreuses au pôle libre de la cellule et colorées violemment en rouge par la réaction de Hotchkiss. Ces granulations sont en outre le siège d'une activité phosphatasique alcaline (les réactions témoins montrent qu'elles sont exemptes de fer et de calcium histochimiquement décelables). Quelques unes de ces granulations se retrouvent dans la lumière des tubules.

Si l'on considère avec Yonge (1926), Coe et Fox (1944) et Coe (1950), les cellules fonctionnelles de la glande digestive des Lamellibranches comme le lieu de digestion intracellulaire des particules alimentaires amenées par les conduits de la glande, l'état de la majorité des tubules, comparable à celui que déclenche un jeûne expérimental, s'expliquerait aisément par la réduction du pouvoir filtrant des moules parasitées et leur état d'inanition. Rappellons cependant, en faveur de la possibilité d'un rôle sécrétoire de la glande digestive, les expériences de Meyer et de Mann (1951) qui démontrent chez les moules parasitées par *Mytilicola* une augmentation du taux de digestion des albumines.

Modifications des autres organes.

Dans les réactions générales de *Mytilus edulis* à la présence de *Mytilicola*, mentionnons également, chez des individus étudiés au mois de Mars, la raréfaction des produits de la gamétogenèse.

Les fonctions d'élimination enfin paraissent très actives, si l'on considère au niveau de l'épithélium rénal le nombre des grains d'excrétion et des granulations de fer qui se trouvent rejetées pas les cellules; celles-ci manifestent en outre la haute activité phosphatasique alcaline déjà décrite chez d'autres Mollusques (G a b e et P r e n a n t, 1949).

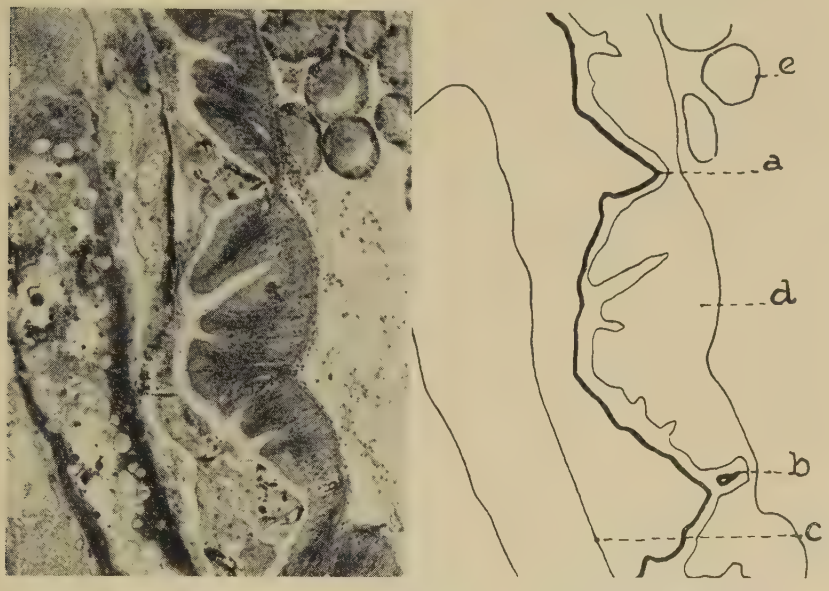

Figure 1. Coupe longitudinale de *Mytilicola* dans l'intestin de la Moule. × 42.
a = appendice thoracique; b = ongle de l'appendice suivant; c = intestin de *Mytilicola*; d = intestin de la Moule; e = tubule digestif de la Moule.

Rapports de *Mytilicola* et de son hôte.

Parmi les dommages causés par *Mytilicola* à son hôte, les méthodes d'investigation histologique et histochimique permettent de mettre en évidence des lésions locales de l'épithélium digestif. Ces petites lésions locales sont déterminées par les mouvements de *Mytilicola* dans l'intestin de la moule. Elles s'observent dans les zones de l'épithélium digestif balayées par les appendices thoraciques et semblent provoquées par les ongles qui terminent ceux-ci. Ces lésions se produisent surtout quand de nombreux *Mytilicola* sont assemblés et comprimés les uns par les autres contre la paroi intestinale, qui apparaît alors privée de son épithélium et dénudée jusqu'à sa membrane basale.

Dans d'autres cas, *Mytilicola* se fixe à la paroi intestinale par ses appendices. Cette fixation doit être durable si l'on en juge par les modifications cellulaires observées dans l'épithélium digestif aux points

où *Mytilicola* implante ses ongles (figure). L'activité phosphatasique alcaline mise en évidence au niveau de ces derniers traduit peut-être une irritation chimique qui se surajoute aux irritations mécaniques produites par l'ongle.

L'étude de *Mytilicola* en place permet enfin de considérer qu'il exerce vis-à-vis de la moule une spoliation de nature alimentaire. Dans la portion de l'intestin où il siège habituellement, le contenu digestif apparaît riche en polysaccharides et, selon la nature des fonds, plus ou moins chargé en calcium et en fer; ces différentes substances, très diluées, sont également mises en évidence dans le tube digestif des parasites (figure). Ceux-ci, situés dans l'intestin moyen et parfois dans l'intestin récurrent, bénéficient des produits de la digestion accomplie par les enzymes de l'estomac et du stylet cristallin.

Les réactions de l'intestin de l'hôte paraissent des plus limitées. Tout au plus peut-on noter une exagération de l'activité phosphatasique alcaline de l'intestin (direct, récurrent, postérieur) dans les zones de contact immédiat avec *Mytilicola*.

Ajoutons cependant que l'épithélium intestinal présente un certain nombre de kystes contenant des *Mytilicola* qui ne doivent pas avoir dépassé le stade nauplius. On sait que les larves naupliennes introduites artificiellement dans la moule ne se développent pas; la réinfestation de l'hôte par des larves issues des sacs ovigères des femelles en place serait donc impossible. Ces formations kystiques de l'intestin sont donc probablement une des rares réactions de défense de la moule contre son parasite.

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Letter to the Editor.

Bingham Oceanographic Laboratory
Yale University, New Haven, Conn.
U. S. A.
1. December 1952

Dear Sir,

A recent paper by E. Steemann Nielsen (*J. Cons.* **18**(2): 117—140, 1952) described a new technique for investigating phytoplankton production in the sea by measuring the accumulation of radio-active carbon (C^{14}). From results obtained during the cruise of the "Galathea", Steemann Nielsen propounded a general estimate of oceanic productivity of about 55 g. carbon per m.^{2} annually fixed by photosynthesis, of which 75 % is assumed to represent net phytoplankton production.

This figure is lower than my previous estimate (Amer. Sci. **32**(2): 129—134, 1944) of 340 ± 220 g. carbon per m.^{2} per year. The latter was based on about 200 experimental determinations of oxygen changes in light and dark bottles containing natural sea water. Of these experiments Steemann Nielsen says, "In America a modification of the method has been used in both eutrophic and oligotrophic regions (Riley, 1938, 1939, 1941a, 1941b), although in the latter with little success, as will be shown in Section 6. In these American investigations it was often not the actual photosynthesis by phytoplankton that was measured, but something else.".

The modification referred to was an increased exposure time, ranging from two days to a week. This is necessary in oligotrophic waters in order to obtain measurable changes in oxygen content. The "something else" is later propounded in these words:— "Thus on the average the rate found for the Indian Ocean is only 4 % of what Riley estimated for the Sargasso Sea. It can hardly have been the intensity of photosynthesis which Riley measured by subtracting the oxygen content in the black bottles from that in the transparent bottles. But what, then, did he demonstrate? Apparently it was simply the bactericidal effect of the sunlight ... It is therefore quite natural that the consumption of oxygen in the transparent bottles should have been lower than that in the black."

Without denying the possibility that the bactericidal effect may produce a significant error, I shall demonstrate by the following examples that the extremity of his position is untenable.

(1) Steemann Nielsen has himself conducted many 24-hour

experiments on oxygen production. His criticism is primarily levelled at experiments lasting more than twenty-four hours. However, in a paper which he finds it convenient to ignore, Riley, Stommel, and Bumpus (*Bull. Bingham Oceanogr. Coll.* **12**(3): 1—169, 1948) subjected all available oxygen production experiments to a detailed ecological analysis, in which it was apparent that experiments of different durations could be combined with no obvious errors. For example, of the experiments at temperatures greater than 20°C., which are particularly pertinent from the standpoint of the discussion of tropical conditions, ten were 5 to 7-day experiments at the Dry Tortugas (Gulf of Mexico) in 1938; fourteen were 2-day experiments in the Sargasso Sea and Gulf Stream system in May 1939. There were twenty-one 3 to 4-day experiments in Long Island Sound in the summers of 1939 and 1940. Of the 24-hour experiments, three were in coastal and slope water in August 1947, and two were in the Sargasso Sea in December 1947. Figure 13 of the paper cited showed the results of the ecological analysis, in which an equation was developed to express oxygen production in terms of phytoplankton concentration, light, temperature, and soluble phosphate. The averages of the groups of experiments, plotted in the figure, differed by little more than 10 %. Within these limits of variation, the highest values were obtained in the 24-hour experiments, the lowest in the one-week Dry Tortugas experiments. If the difference is significant, it is the opposite of what Steemann Nielsen's hypothesis would predict.

(2) Speaking in more general terms, the analysis as a whole included over 200 experiments of various durations and in areas ranging from the temperate region of the western North Atlantic to the tropics. All of them fell into a rational scheme of analysis except 56 24-hour experiments on Georges Bank in September 1939 and June 1940. In these it seemed likely that some nutrient other than phosphate was the most important limiting factor. If Steemann Nielsen's hypothesis were correct, it would indeed be a remarkable coincidence that the bactericidal effect of light is influenced by precisely the same group of factors, including phosphate and phytoplankton concentration, that one ordinarily proposes for the examination of phytoplankton photosynthesis and growth.

(3) His argument is facilitated by the fact that there is frequently a decrease in oxygen content in both light and dark bottles. This sometimes occurs in 24-hour experiments, and it tends to become more pronounced with longer exposure, presumably because of the well known phenomenon of bacterial multiplication in stored sea water. Steemann Nielsen has found it expedient to regard this multiplication as occurring only in the dark bottle in near-surface exposures, thus invalidating the use of the difference between light and dark bottles as an indicator of photosynthesis. Typical examples of the kind of experiment that he regards as spurious are fourteen 5 to 7-day experiments conducted off the Dry Tortugas (*J. Mar. Res.* **1**(4): 335—352, 1938). The mean oxygen production at the surface was 1·25 mg.

per litre per week; the mean oxygen consumption in the dark bottle was 1·21 mg. Presumably Steemann Nielsen would regard photosynthesis as little more than the observed net increase af 0·04 mg. per litre in the light bottle. But let us examine the experiments in detail. In seven of them there was an increase in the light bottle ranging from 0·08 to 0·83 mg. O_2 in a week's time and averaging 0·39 mg. These figures are well above the limits of analytical error; they are cleared of the argument of bactericidal effects. They represent the excess of photosynthesis over the respiration of the enclosed biological community and hence can be regarded only as a minimum estimate of the total phototynthesis. However, for purposes of argument let us accept this figure and furthermore assume that photosynthesis was zero in the seven bottles that showed a net decrease in oxygen. The average for the whole series is then 0·195 mg. O_2 per litre per week. The calculated carbon production is 0·01 mg. per litre per day, a figure ten times Steemann Nielsen's mean value for stations 265—274 in the Indian Ocean, which he used for a detailed comparison of the results of the two methods. Whether this indicates a different order of magnitude of productivity in the two areas or a serious error in the C^{14} method remains to be seen.

It is not necessary to admit, except for purposes of numerical exposition, that photosynthesis was negligible in the seven cases of net decrease of oxygen in the light bottle. Three of them (controls in experiments 1—3, Table VII of the paper cited) were accompanied by measurements of phytoplankton pigments (Harvey method) in initial, light, and dark bottles. All showed an increase in the light bottle, with the total production ranging from 50 % to 150 % of the initial population. The decrease in oxygen ranged from 0·05 to 0·34 mg. By Steemann Nielsen's criterion, photosynthesis was negligible, but under the circumstances one can hardly imagine that such was the case.

(4) In four of the Dry Tortugas experiments, water samples were taken from depths of 1, 5, 10, and 15 m., were drawn off into light and dark bottles, and were returned to the depth of capture for a one-week exposure. Detailed results are listed in the paper cited. It suffices here to say that the average net increase in oxygen in the light bottles was as follows:—

Depth, m.	1	5	10	15
Mg. O_2 per litre per week	0·165	0·325	0·577	0·602

While Steemann Nielsen was conveniently vague about the probable depth-range of his hypothetical bactericidal effect of light, one supposes that bacterial mortality might decrease with increasing depth. However, I look in vain for evidence that increasing bacterial respiration was reducing the net increase of oxygen in the deeper experiments. Furthermore, let us assume that (a) the bactericidal effect was fully operative at the surface, so that total photosynthesis was little more than the observed net increase of 0·165 mg.; (b) the bactericidal

effect was relatively insignificant at 15 m., so total photosynthesis may be expressed by the difference between light and dark bottles, which averaged 1·04 mg. per week. These assumptions are consistent with Steemann Nielsen's hypothesis, but the numerical results cannot be accepted without proof. It is common to find a slight increase in photosynthesis with depth in the surface layer, but a six-fold increase has never been reported and seems improbable.

Although the attack on the oxygen method seems as empty as it is violent, it is immediately apparent that the new C^{14} technique is superior in sensitivity and accuracy. Steemann Nielsen is to be congratulated for introducing a powerful new tool to marine biology. However, one might wish he had spent more time experimenting with the method before using it on a long and important expedition, since there is some doubt as to the validity of his interpretation of the results. For example, he admits that the loss of C^{14} by respiration invalidates the method at low light intensities; but in the subsequent analysis of experimental data taken at sea, there is no evidence that he attempted to allow for an increasing error at illuminations of 10 % and 1 % of the surface light. Nor did he appear to recognize the possibility that variations in temperature and nutrient supply could affect the relation between photosynthesis and respiratory loss. There is a further loss if protozoa and other small zooplankton complete the degradation of significant amounts of phytoplankton during the course of the experiment, although this may be a minor effect in short-period experiments. Probably in most cases the results of the C^{14} method fall somewhere between the net phytoplankton production and total photosynthesis, but exact evaluation of the meaning of the experiments will require an extensive experimental programme.

Finally, we come to the question of general oceanic productivity. In the Indian Ocean, Steemann Nielsen listed 29 C^{14} experiments in which the estimated carbon production ranged from 85—400 mg. per $m.^2$ per day, with a mean of about 190 mg. In 58 experiments in the eastern Atlantic reported in *Nature* (**167**: 684—686, 1951), there was a range of 20—2000 mg., and a "production of 100—200 mgm. carbon per square metre per day was most commonly found". From these and presumably other experiments not yet reported in detail, he arrived at a general figure of about 150 mg. carbon per $m.^2$ per day.

In 1944 (*Amer. Sci.* paper cited above), I listed seven areas in the Atlantic Ocean in which photosynthesis was estimated to range from 165 to 1550 mg. carbon per $m.^2$ per day and net phytoplankton production 14—1000 mg. Acknowledging that it was a small group of data and a limited number of regions, I made no attempt to derive an exact estimate of oceanic productivity. Rather, I suggested that the most probable value was 340 ± 220 tons of carbon per $km.^2$ per year (ca. 300—1500 mg. per day).

From these data and discussions, Steemann Nielsen derived the rather questionable conclusion that his estimate is a whole order of magnitude lower than mine. I should prefer to conclude that (a) the

extreme ranges established by the two methods are nearly the same; (b) there is no reason to doubt the essential validity of either experimental method; and (c) it remains for the future to determine a reasonable average value for productivity. It is becoming increasingly clear that large variations occur in subtropical and even in tropical waters, so that we must study oceanic waters as closely as we examine our temperate coastal regions in order to arrive at an accurate estimate of their productivity. In support of this point (which may be regarded as an apology for the optimism of my earlier years as well as a reproach to Steemann Nielsen) I shall conclude with a brief account of some researches on the Sargasso Sea, one of those blue, oceanic wastes where one might suppose that life proceeds slowly and evenly.

A series of stations in May 1939 revealed a total phytoplankton population that seemed surprisingly large for subtropical waters. The average estimate of photosynthesis based primarily upon surface oxygen experiments was nearly 1·5 g. carbon per m.^{2} per day, a figure later derided by Steemann Nielsen, who suggested that 110 mg. is a more reasonable average figure.

In August 1947 (Riley and Gorgy, *J. Mar. Res.* **7**: 100—121, 1948) the total population was nearly an order of magnitude lower. Photosynthesis was undetectable by oxygen experiments. By indirect physical oceanographic methods it was estimated that carbon production in the upper 75 m. in excess of the immediate respiratory needs of the community inhabiting the same stratum was of the order of 50 mg. per m.^{2} per day. In December 1947 both the phytoplankton population and its photosynthetic activity were of the same order of magnitude as in May 1939.

More recently, through the kindness of the U. S. Coast Guard, a two-year series of weekly plankton collections has been obtained at a weather station in the north-central Sargasso Sea (35°N., 48°W.). Examination of the series has revealed a pronounced seasonal variation, with very small populations of 1000 cells per litre or less in summer, a small but distinct spring flowering with a maximum concentration of the order of 70,000 cells per litre, and other flowerings of a more random character, particularly in late autumn and early winter.

It remains to establish a reasonable average value for the productivity of the Sargasso Sea within the wide limits quoted above. The only method that presents itself at the moment is a consideration of plankton dynamics. The average zooplankton population is of the order of 50 ml. displacement volume per m.^{2}. Some 20 experiments on the oxygen consumption of Sargasso Sea zooplankton indicate an average daily carbon requirement of about 0·6 % of the displacement weight (volume). Thus it would appear that an average phytoplankton production of about 300 mg. carbon per m.^{2} per day is necessary to supply zooplankton food requirements. The photosynthetic production of carbon must be somewhat larger, probably at least 400 mg. per day.

Respectfully submitted,

Gordon A. Riley.

Obituary.

We regret to announce the deaths of Professor Francesco Vercelli, Director of the Istituto Talassografico, Trieste, on 24. November 1952; and of Dr. J. H. Orton, F. R. S., Professor Emeritus of Zoology in the University of Liverpool, on 2. February 1953.

Reviews.

T. Braarud and **E. Føyn.** "Nitrite in polluted sea-water, observations from the Oslo Fjord 1946—1948." Avhandl. utgitt av Det Norske Videnskaps-Akademi i Oslo, I. Mat.-Naturvid. Kl., No. 3, pp. 1—24, 17 figs. Oslo 1951.

Sewage from Oslo is discharged to the Oslo fjord. Previous work on the extent of pollution has been made by studying the distribution and density of phytoplankton and the concentration of oxygen in the water. In the present work the concentration of nitrite was used as a possible index of pollution and results of determinations made on samples of water taken at different seasons from the surface and from deeper layers in the fjord, inland from Drøbak sound, are shown in tables and graphs and are compared with results of the earlier work. Relatively unpolluted coastal waters around Norway usually contain less than 4 mg. nitrite per cu.m. In the western branch of the inner fjord furthest from the source of pollution by sewage, the nitrite content of the surface layers was low during summer and higher (5—12 mg. per cu.m.) during autumn and winter. The deeper layers were poor in nitrites except in November and April when the concentration was about 6 mg. per cu.m. In Oslo harbour, values for the surface layers were high; the concentration varied from 7 mg. to 20 mg. per cu.m. except in May when values were lower; in summer there was a decrease in concentration with depth to 10 m. and then an increase with depth to 20 m.; in winter the lowest values were obtained at depths of 20 m.; during March the water mass under ice was rich in nitrite (19·5 mg. to 27·5 mg. per cu.m.). In the eastern branch of the fjord distribution was similar to that in the western branch except during March when the concentration at the surface and in the deep layers was extremely high; this is attributed partly to an influx of water rich in oxygen which mixes with stagnant layers and brings about oxidation of ammonia and possibly also increased decomposition of organic matter, and partly to ice-bound conditions which reduce dispersal of the polluting materials. The relative importance of nitrifying bacteria and nitrate-reducing bacteria in forming nitrites and the effects of consumption of nitrites by phytoplankton on the seasonal distribution are discussed. It is concluded that the high nitrite values obtained for surface samples are characteristic of the highly polluted waters in Oslo harbour throughout the year and that this value for concentration of nitrite would be a useful criterion for assessing pollution in that area. In other circumstances the concentration of nitrite may be more closely related to the effects of biological activity than to direct pollution by sewage.

E. Dawson.

Douglas P. Wilson. "A Biological Difference between Natural Sea Waters." Journ. Mar. Biol. Assoc. U. K., **30**, 1, pp. 1—20. Cambridge, 1951.

Die vorliegende Arbeit bietet einen interessanten Beitrag zur Frage des unterschiedlichen Verhaltens der Wassermassen im Gebiet vor der südwestenglischen Küste. Schon seit über einem Jahrzehnt ist durch die Untersuchungen der englischen Forscher F. S. Russell, W. R. G. Atkins, H. W. Harvey und L. H. N. Cooper bekannt, dass in biologisch-chemischer Hinsicht grosse Unterschiede zwischen den Wassermassen vor der südwest-englischen Küste bestehen und dass seit etwa 1930 starke Verschiebungen in der Lage dieser Wassermassen stattgefunden haben. Der Verfasser hat eine grosse Anzahl sehr sorgfältig überwachter Kulturversuche an Eiern und Larven der Meeres-Invertebraten *Echinus esculentus*, *Ophelia bicornis*, und *Sabellaria alveolata* durchgeführt. Dabei hat sich ergeben, dass der Entwicklungsgang in Meerwasserproben, die aus dem Englischen Kanal in der Gegend von Eddystone entnommen waren,[1]) regelmässig anomal verlief und die Organismen frühzeitig abstarben. Im Gegensatz hierzu verlief die Entwicklung unter gleichen Verhältnissen in Wasserproben aus der Keltischen See zwischen Südwest-England und Süd-Irland völlig normal[2]). Da irgendwelche chemische oder physikalische Änderungen der Wasserproben infolge der Vorbehandlung mit grosser Wahrscheinlichkeit auszuschliessen sind, kommt der Verfasser zu dem Schluss, dass die Ursachen der Schädigung der Organismen in dem Kanalwasser selbst zu suchen sind. Und zwar hat es den Anschein, als ob in dem Kanalwasser entweder Spuren gewisser giftig wirkender Substanzen vorhanden sind, oder, was wahrscheinlicher ist, dass ein oder mehrere Spurenelemente oder organische Verbindungen, die für die Entwicklung des Lebens unentbehrlich sind, fehlen. Die Ergebnisse dieser Untersuchungen liegen mit den übrigen aus diesem Meeresgebiet bekannten chemischen und biologischen Befunden in gleicher Richtung.

K. K.

L. H. N. Cooper. "Factors Affecting the Distribution of Silicate in the North Atlantic Ocean and the Formation of North Atlantic Deep Water.". Journ. Mar. Biol. Assoc. U.K., **30**, 3, pp. 511—526. Cambridge 1952.

Untersuchungen der R. R. S. "Discovery II" im Mai 1950 am südwesteuropäischen Kontinentalabhang westlich Ushant haben zu dem bemerkenswerten Ergebnis geführt, dass im Tiefenwasser unterhalb 2000 m. mit zunehmender Tiefe der Silikatgehalt in erheblichem Masse ansteigt (von etwa 20 auf 40 g.-atom/L), während die entsprechenden Werte im Salzgehalt, in der Temperatur, sowie in der Dichte und auch im Gesamt-Phosphor-Gehalt nur geringfügige Änderungen aufweisen. Auf Grund unserer bisherigen Kenntnisse vom Verhalten des nordost-atlantischen Tiefenwassers ist dieser Befund nur schwer verständlich. Jedenfalls lässt er sich durch einen einfachen Zumischungsvorgang von Mittelmeerwasser aus der Strasse von Gibraltar zu nord-atlantischem Tiefenwasser nicht ohne weiteres erklären. Da bisher vom offenen Ozean noch zu wenig verwertbare Silikat-Bestimmungen vorliegen, die diesen Befund deuten lassen, stellt der Verfasser 5 Hypothesen auf, die

[1]) in sogenanntem "*Setosa*-Wasser" nach dem Vorkommen der charakteristischen Leitform *Sagitta setosa*.

[2]) in sogenanntem "*Elegans*-Wasser" nach dem Vorkommen der charakteristischen Leitform *Sagitta elegans*.

für eine Erklärung in Frage kommen. Es sind dies folgende Möglichkeiten. 1) Lösung von Silikat aus Bodensedimenten, 2) Lösung aus Ton oder Siliciumverbindungen, die sich in Suspension im Meerwasser befinden, 3) Anreicherung durch einen vertikalen Kreislauf des Meerwassers, wie wir es aus dem antarktischen Meeresgebiet kennen, 4) Entwässerung der silikatreichen Tundrengebiete, 5) Absinkvorgänge von Oberflächenwasser. Eine klare Entscheidung über die Art und Grösse der Beteiligung dieser Vorgänge ist ohne zahlreiche weitere Silikat-Untersuchungen im nord-atlantischen Raum nicht möglich.

K. K.

H. L. N. Cooper. "Chemical Properties of the Sea Water in the Neighbourhood of the Labadie Bank." Journ. Mar. Biol. Assoc. U. K., **30**, 1, pp. 21—26. Cambridge, 1951.

Der Verfasser gibt einen kurzen Bericht über die Art der Gewinnung und das Ergebnis der chemischen Messungen der Wasserproben aus der Keltischen See, die von D. P. Wilson (siehe vorhergehende Besprechung) bei seinen Untersuchungen an Invertebraten-Eiern und Larven benutzt wurden. Es handelt sich um drei Wasserproben. Zwei davon stammen aus dem Gebiet der Labadie-Bank. Alle drei Wasserproben scheinen auf Grund der chemischen Untersuchungsbefunde aus Gebieten zu stammen, in denen eine rege Regeneration des Phosphats aus dem detritusreichen Schlick am Meeresboden stattfindet.

K. K.

L. H. N. Cooper. "Processes of Enrichment of Surface Water with Nutrients due to Strong Winds Blowing on to a Continental Slope." Journ. Mar. Biol. Assoc. U. K., **30**, pp. 453—464, 4 figs. Cambridge, 1952.

L. H. N. Cooper. "The Physical and Chemical Oceanography of the Waters Bathing the Continental Slope of the Celtic Sea." Journ. Mar. Biol. Assoc. U. K., **30**, pp. 465—526, 15 figs. Cambridge, 1952.

Beide Arbeiten befassen sich mit ozeanographischen Verhältnissen am Kontinentalabhang vor der "Keltischen See". Dabei wird nach L. H. N. Cooper und D. Vaux (Journ. Mar. Biol. Assoc. U. K., Vol. **28**, 1949) als Keltische See das Gebiet südlich von Irland und vor dem Westausgang des Englischen Kanals bis zum Schelfrand bezeichnet.

Die erste Arbeit liefert einen Beitrag zur Erklärung der Anreicherung an Nährstoffen im oberflächennahen Wasser. Es wird auf die Möglichkeit einer internen Brandung (capsizing) hingewiesen, von der angenommen wird, dass sie bei auflandigen Stürmen unterhalb der homogenen winterlichen Deckschicht, die bis 100—200 m. Tiefe in diesem Gebiet reicht, entstehen kann. Wenn ein solcher Vorgang wirksam wäre, würde er mit starker vertikaler Mischung und dadurch mit einer Zufuhr von Nährstoffen in Oberflächennähe aus dem nährstoffreichen Wasser unterhalb der Deckschicht verbunden sein.

Eine Bestätigung der internen Brandung durch Beobachtungen wird nicht erbracht. Dazu sei bemerkt, dass der eindeutige Nachweis von interner Brandung sich bisher nur auf Fälle mit starker Strom- und Dichteschichtung bezieht, wie z. B. in der Strasse von Gibraltar und in der Strasse von Messina, (A. Defant, Arch. f. Meteorol., Geophys. u. Bioklimat., **1**, 1949).

Bei dem sehr schwachen Dichtegefälle, das unter der homogenen Deckschicht im Gebiet des Kontinentalabhanges vor der Keltischen See, wie in der ganzen Biscaya besteht, erscheinen die physikalischen Voraussetzungen für die Entstehung einer internen Brandung kaum erfüllt. Zum gleichen Endergebnis,

nämlich der beobachteten Anreicherung von Nährstoffen in Oberflächennähe, führt die winterliche Konvektion, die bei dem geringen Dichtegefälle eine verhältnismässig tiefreichende Schicht erfasst.

Die zweite Arbeit verfolgt einen doppelten Zweck. Einmal wird versucht, an Hand der vorliegenden ozeanographischen Beobachtungen die Wasserkörper vor dem Kontinentalabhang der Keltischen See zu charakterisieren. Dabei wird von der Beziehung Temperatur—Salzgehalt bis zu Tiefen von 2000 m. ausgegangen. Ausserdem werden Nährstoff- und Sauerstoffgehalt der Wasserkörper berücksichtigt, soweit es die fragmentarischen Beobachtungen zulassen. Die Darstellungen sind darauf gerichtet, dem Meeresbiologen eine Vorstellung von dem hydrographischen Hintergrund der biologischen Vorgänge in der Keltischen See und im Englischen Kanal zu ermöglichen.

Ferner wird mit der Arbeit angestrebt, den *status quo* der hydrographischen Kenntnisse dieses Seegebietes festzuhalten, um damit dem Ozeanographen bei den vielfältigen Problemen in diesem Seegebiet eine Ausgangsbasis für künftige Untersuchungen zu bieten.

Fünf Hauptwasserarten werden unterschieden, von denen vier im wesentlichen in Übereinstimmung zu den atlantischen Wasserkörpern stehen, die G. Wüst und A. Defant ("Meteor"-Werk, **6**, 1936) angeben, nur dass andere Bezeichnungen gewählt wurden (North Atlantic deep water: mittleres atlantisches Tiefenwasser, Gibraltar water: oberes atlantisches Tiefenwasser, North Atlantic central water: subtroposphärisches Wasser, Layer of winter mixing: Deckschicht). Der fünfte Wasserkörper (Local capsized and cascaded water) stellt Mischwasser am Kontinentalabhang dar. Wenn man die Rolle der internen Brandung noch als problematisch ansieht, so liegt das Hauptgewicht der Erklärung auf den Abgleitvorgängen (cascading effect). Es handelt sich um das Abgleiten des winterlich ausgekühlten Wassers, das vom Schelf am Kontinentalabhang absinkt bis in eine Tiefenlage, die der Dichte dieses Wassers entspricht (in 400—800 m.).

Die örtlichen Erscheinungen des Abgleitens und sein jährlicher Gang werden speziell betrachtet, und zwar an Hand der älteren Beobachtungen von "Thor" 1906, "Armauer Hansen" 1914, der neueren Beobachtungen von "Discovery II" und "William Scoresby" 1950 sowie von der irischen Terminstation SS aus der Zeit 1910—1934. Die unterseeischen Cañons, die 1949 von dem englischen Vermessungsschiff "Dalrymple" erlotet wurden und die ausschnittsweise in einer Tiefenkarte wiedergegeben sind, werden als vorgegebene Wege für das abgleitende Wasser vermutet.

Mehrere Teilprobleme der physikalisch-chemischen Ozeanographie des behandelten Seegebietes werden angeschnitten, aber der lückenhafte Stand der Beobachtungen erlaubt nur vereinzelt gesicherte Aussagen. Bei der Bedeutung der Vorgänge am Kontinentalabhang für die Ozeanographie des angrenzenden Schelfmeeres bleibt zu wünschen, dass die mannigfaltigen Anregungen, die die Arbeit von L. H. N. Cooper bietet, zu einer stärkeren Berücksichtigung der Schelfränder in den Untersuchungsprogrammen beiträgt. *G. Dietrich.*

S. M. Miller. "Phosphorus exchange in a sub-tropical marine basin." Bull. Mar. Sci. of the Gulf and Carribbean, Vol. **1**, No. 4, pp. 257—265, 5 figs. Miami, 1952.

The total phosphorus in the sediment and in the overlying water of a shallow marine basin was determined periodically during 1950 and 1951, for the purpose of detecting any phosphorus exchange taking place between sediment and water.

The basin or harbour with a depth of 18 feet in the centre is connected with Biscayne Bay by a narrow channel some 8 feet deep. The rise and fall of tide is small; the salinity of the water higher in summer than in winter; the water is stratified. The bottom deposit is soft, one gramme of dry matter occupying a volume of 2 ml.

The hydrogen-ion-concentration was notably low, indicating considerable decomposition of organic matter taking place throughout the year; the pH of the water varied regularly from 7·6 in summer to 7·85 in winter while that of the sediment varied in the same way from 7·5 to 7·7.

The total phosphorus in the water was remarkably high— between 4 and 5 mg. atoms (120—150 mg.) P per $m.^3$ in summer, falling in a uniform manner to between 2 and 3 mg. atoms in the winter. It is not stated how much of this was in solution and how much in suspended detritus.

Conversely the phosphorus content of the sediment, collected to a depth of about 5 cm. with a grab, increased in a uniform manner by 4 to 5 per cent. from summer to winter, falling again between winter and the following summer to the lower value.

An exchange between sediment and water is considered to have taken place in the following way. In the spring and early summer the warm, relatively calm weather may have caused anaerobic conditions in the top layer of sediment, reducing ferric phosphate to the soluble ferrous which would precipitate as iron sulphide, leaving inorganic phosphate in solution.

However, there is no statement in this paper that the increase in total phosphorus in the water between winter and summer was due to an increase in dissolved inorganic phosphate. Walton Smith, Williams, and Davis (Ecology **31**, p. 124, 1950) found low values of phosphate-phosphorus in the surface water of this harbour throughout a year, never more than 0·03 mg. atoms phosphate P per $m.^3$. This suggests that nearly all the total phosphorus found in the water (4—5 mg. atoms) may have been present as dissolved organic phosphorus and in particles of detritus, and that the detritus in suspension varies with the seasons.

H. W. H.

K. Wyrtki. "Der Einfluss des Windes auf die Wasserbewegung durch die Strasse von Dover." Deutsche Hydrogr. Zeitschr., **5**, 1, pp. 21—27, 8 figs. Hamburg, 1952.

In his introduction the author differentiates between two possible causes of residual flow through the Straits of Dover, namely (1) an *in situ* drift current produced by local winds, and (2) gradient currents as a result of winds over distant sea areas. He then relates Carruthers's current measurements made at the "Varne" lightvessel to wind as deduced from pressure gradients over the southern North Sea. He points out that because the residual flow represents only about 10 % of the instantaneous flow, it seems advisable to limit the investigation by the use of monthly averages of wind and current. To obtain a general picture, however, the frequencies of the three-day values of current for the period 1926—1934 and the monthly averages of wind for the thirty years 1916—1945 have been compared in a diagram. This is not intended to show the dependence of currents on wind, since the two periods are not concurrent, and also, as the author later indicates, the winds during the current-observation period (1926—1938) were not typical of the longer period 1901—1930. From this general picture, however, the effect of bottom configuration on the direction of flow is apparent.

Dr. Wyrtki continues by making a correlation between the south-westerly component of the monthly averages of wind and the component of current along the main current direction of N.19°E. for the period 1926—1938. The use of monthly averages does not permit one to distinguish between linear and non-linear dependence of the variables in this case. In the author's opinion, the correlation coefficient of 0·72 is satisfactory under the conditions prevailing, for, as he states, the current produced by a given wind depends on the previous history, and also a given current does not necessarily result from a unique value of the wind. He gives a diagram which may be used to forecast the average current produced by an average wind, taking into account all of these considerations.

The actual direction of the current is thought to be independent of the wind direction, but related to wind strength in that an increase in strength in the prevailing south-westerly wind results in a clockwise rotation of the residual current. Wyrtki thus arrives at the important conclusion that fluctuations in current direction at the "Varne" lightvessel are due to variations, not of wind direction, but of wind strength.

Wyrtki next investigates a possible relation between currents and salinity as measured at the "Varne". Apart from a lowering of the salinity in general when winds have two to four weeks previously been from the north or from the east, in which case river water from the Thames or the Rhine and the Schelde, is driven towards Dover Strait, there is no apparent relation.

Finally, two examples are given to show how the movement of water may be estimated by following a "front" or a "patch" of water of known salinity. In each case there is agreement between the predicted and measured values. A word of warning should be given here, however. It is not *always* safe to trace water by a characteristic property unless one can be sure that the property is conservative. The salinity of a patch of water may be reduced by mixing or excess of rainfall over evaporation, or it may be increased if evaporation predominates. Examples of this are not uncommon in the southern North Sea, and the above method, if applied during the winter of 1946—47, would certainly have led to a wrong estimate of residual drift. In the English Channel, and especially if the estimate is confined to the rate of progress of Atlantic water up-Channel during summer months, Wyrtki's method is probably satisfactory, but the fact that water from the western part of the Channel may rise to the surface in the eastern Channel, as pointed out by Lumby (M. A. F., Fishery Invest., Ser. II, **7**, No. 7, 1925) may again give rise to an erroneous value of drift.

Dr. Wyrtki's paper is a welcome addition to the literature on wind—water relations and should stimulate those interested in this branch of science to further efforts.

David Vaux.

O. Bjørgum. "On energy transformations and the effect of fluctuating pressure gradients in turbulent shear flow." Universitetets Årbok 1951, Naturvit. rekke, No. 3, pp. 1—18, 2 figs. Bergen, 1952.

In this paper, the author considers turbulent pressure flow between parallel planes. The energy-balance of a fluid element is derived, using Taylor's result for the rate at which the mean flow transfers energy to the turbulence. However, the derivation contains an error which is equivalent to assuming that the fluctuating pressure forces do no work, and the author's claim that Kolmogoroff's theory of local isotropy requires the work done by the pressure to vanish is not valid. Later sections of the paper are based largely

on these erroneous results, though the conclusion that the work done by individual components of the fluctuating pressure forces cannot be neglected appears to be justified by the experimental evidence. *I. P.*

O. Bjørgum. "On the steady turbulent flow along an infinitely long smooth and plane wall." Universitetets Årbok 1951, Naturvit. rekke, No. 7, pp. 1—14, 3 figs. Bergen, 1952.

In the absence of mean pressure forces in flow along an infinite plane boundary, the author derives, on the basis of similarity and dimensional reasoning, the usual logarithmic mean velocity profile for the flow outside the viscous layer near the boundary. The argument is essentially the same as that given in recent years by Squire (Phil. Mag., 1948, p. 1).

In the layer of viscous flow near the boundary, the formula

$$K = \varkappa^2 U^2 \Big/ \left|\frac{dU}{dy}\right|$$

is suggested for the eddy-viscosity K, where U = mean velocity, y = space variable perpendicular to the boundary, and $\varkappa$ = numerical constant. The resulting equation for the mean flow is solved, and it is concluded from a comparison with experiment that Karman's similarity theory gives a better approximation to the solution in the outer regions of the viscous layer. By joining these two solutions in a suitable manner, a velocity profile in good agreement with experiment is obtained. However, the treatment of the viscous layer is somewhat empirical, and it is doubtful whether the agreement with experiment has any particular significance. *I. P.*

O. Bjørgum. "On the analogy between turbulent transfer of heat and momentum." Universitetets Årbok 1951, Naturvit. rekke, No. 10, pp. 1—8. Bergen, 1952.

The equation for the turbulent transfer of the square of the fluctuating temperature in plane shear flow is written out to illustrate the limitations of Reynolds's analogy between the transfer of heat and momentum. Thus when the Prandtl number σ is unity and there are no mean pressure forces, the presence of fluctuating pressure gradients prevents heat and momentum being transported in the same way unless there is a suitable distribution of heat sources. The author's remarks concerning the similarity of transfer of heat and momentum in the special case $\sigma = 1/3$ are based on an invalid deduction from Kolmogoroff's theory of local isotropy. *I. P.*

Günter Dietrich. "Oberflächenströmungen im Kattegat, im Sund und in der Beltsee." Deutsche Hydrogr. Zeitschr., **4**, H. 4/5/6, pp. 129—50. Hamburg, 1952.

R. Kändler. "Der Einfluss der Wetterlage auf die Salzgehaltschichtung im Übergangsgebiet zwischen Nord- und Ostsee." Deutsche Hydrogr. Zeitschr., **4**, H. 4/5/6, pp. 150—60. Hamburg, 1952.

The Transition Area between the North Sea and the Baltic has often attracted the interest of hydrographers and marine biologists. The multitude of factors determining the events, and the changeability in place and time of the hydrographic situation make it a rather difficult task to describe the

currents between the North Sea and the Baltic and to give a proper explanation of the causes. The attention paid to this area is partly the result of the existence of a dense system of observation positions, which covers the coasts of Denmark, Germany, and Sweden.

Starting from Mangold's and Wattenberg's famous investigations G. Dietrich and R. Kändler have attacked the problem in two independent papers, one dealing with the surface currents, and the other with the structure of the water masses and their movements. As both direct attention to the interaction of the synoptic weather situation and the hydrographic situation and its changes, they may be reviewed together.

Günther Dietrich confines his investigations to the surface currents. By using statistical methods 30,000 current measurements and 4,000 air-pressure observations taken during 1937 are examined. Short-time variations are neglected by taking average values for a day; this was possible, as the Danish and German lightships measure the current four times a day. The daily mean gradient of the air pressure was calculated for the whole area. These mean values are the basic data for the investigation. First, the relationships between wind and current-direction are investigated by graphical evaluation. Then the effect of the wind velocity on the current velocity is studied for 12 different sections covering the whole compass, each section being of 30°. The results of the correlations are given as diagrams for 10 lightships, from which, if wind-direction and velocity are known, the corresponding current-direction and velocity can easily be read off. Two charts show the surface current for the area investigated for the four main wind-directions for Beaufort forces 3 and 6 respectively.

The results of the correlation of wind and current are discussed separately for the Belts and the Sound, where they are fairly easy to appreciate. Only two directions of current are possible, the currents are subject to the same air-pressure gradients (mostly with due east and west winds), and on days without winds the outflow from the Baltic is predominant. The outflow ceases with winds of 1—3 Beaufort. At all other places in the Transition Area, not only wind and gradient currents prevail, but also convection currents. The bottom topography and the coast line make the picture more complex. Dietrich tries to give satisfactory explanations for the unexpected currents at Skagen Rev, Læsø Trindel, and Anholt Knob, which of course must be only qualitative.

For nautical purposes the charts and diagrams are very useful. They give average values based on empirical correlation. But an understanding of the events is only partly attained. In the relation of wind and currents not only direction and velocity are of importance but also duration. This, I suppose, could not be dealt with by studying only one year and to do so would have enlarged the work considerably. But it may be hoped that the continuation of the paper as announced will stress also this factor in the interrelation of meteorological and hydrographical phenomena.

The other paper, also based on observations in 1937, shows how the internal hydrographic situation in the same area is affected mainly by three types of weather condition. This paper is a continuation of Wattenberg's famous work in the Transition Area. For biologists mean values of temperature and salinity are more or less worthless. For ecologic studies the extreme values must be known, as they indicate the conditions when halophilic forms can enter a region usually populated by organisms preferring fresh or brackish water. But a better understanding of the mechanism of the hydrography is gained by the study of the actual situations. Kändler's paper shows

clearly that the duration and force, besides the direction, of the winds affect the water exchange between the Skagerak and the Baltic.

Kändler distinguishes three types of weather situation creating particular hydrodynamic situations. High air-pressure over central Europe, causing light winds in the Transition Area, enables an undisturbed exchange of the water masses to take place. Outgoing currents in the surface layers and inflow into the Baltic in the deeper water layers, as well as very stable stratification in the Belts, characterize this situation. In the Kattegat only two water masses exist, the Baltic and the Skagerak waters, with a very sharp discontinuity layer (20 to 32 ‰ salinity) which starts at the surface at the boundary between the Skagerak and Kattegat, but in the Kattegat is at about 10 to 15 m. deep. In the south of the Belt this layer is split up, but sometimes reaches the Askona Sea and in that way transports high-salinity water into the Baltic.

With stronger winds a third type of water mass is created by turbulence in the Kattegat. If the winds blow from the east, the Baltic waters may be forced into the Belt, and the Skagerak front is thrust out into the Skagerak; no inflow of water of high salinity takes place. This situation develops mostly during March and November.

The third type of weather situation is characterized by a strong cyclonic activity over Scandinavia. In this case Kattegat water is formed by turbulence. The Skagerak front enters the Kattegat and the Belt front is thrust out into the Baltic. With a long period of westerly winds the discontinuity layer disappears completely and the salinity decreases gradually from the Skagerak towards the Baltic, the isohalines being vertical.

Both papers complement each other, in showing that no average situation exists in the Transition Area. The surface current can be correlated with the winds by appropriate statistical treatment, but a description of the events in the deeper layer can only be approximated by classification in a few main types.

Finally, a remark about the name of the area under consideration. It is agreed, as Dietrich states, that Transition Area is not a proper geographical name, but from the hydrographical and biological point of view it seems the most adequate and so is used by the Council. It emphasizes the intermediate nature of the area and its liability to change. In this sense it was also used by Kändler in "Übergangsgebiet zwischen Nord- und Ostsee".

F. F. K.

Juliette Lecal-Schlauder. "Recherches morphologiques et biologiques sur les coccolithophorides Nord-Africains." Ann. Inst. Océanographique, **26**, pp. 255—362. Paris, 1951.

The coccolithophorids represent a group of plankton organisms which is still to a great extent unexplored — and for good reasons. Most of the species are small and it takes much time, patience, and skill to obtain information on their taxonomy and biology. Moreover, the Mediterranean is classical ground for studies of this group. Nevertheless, Lecal-Schlauder in her monograph of North African coccolithophorids has brought forward a wealth of new information on their morphology and distribution.

Thirty-four new species and forms, belonging to 16 genera, and 10 species which were previously unsatisfactorily known, are described and instructive sketches are given of the cells and coccoliths. Two new genera, *Clavosphaera* and *Bernardosphaera*, are created. A key to the 162 species of marine coccolithophorids which seem to be well established is given on the basis of a

taxonomic division into 5 families. A detailed account of the seasonal and vertical distribution of the coccolithophorids of the bay of Algiers and additional observations from a number of other North African waters are given, and comparison made with observations in other parts of the Mediterranean.

A valuable chapter is also included on the cytology of the various species, containing information on mitosis, formation of coccoliths, storage products, etc., and a comparison is made with the Chrysomonadineae and the Cryptomonadineae.

The monograph contains so much new and so much up-to-date information from scattered publications that it is bound to be of great value to everybody who works on marine phytoplankton, even in quite different regions.

Trygve Braarud.

J. N. Carruthers, A. L. Lawford, V. F. C. Veley, and **B. B. Parrish.** "Variations in brood strength in the North Sea haddock, in the light of relevant wind conditions." Nature, **168**, pp. 317-19, 2 figs. London, 1951.

J. N. Carruthers, A. L. Lawford, and **V. F. C. Veley.** "Fishery hydrography: brood-strength fluctuations in various North Sea fish, with suggested methods of prediction." Kieler Meeresf., **8**, 1, pp. 5—15, 15 figs. Kiel, 1951.

These two papers are of considerable interest because they represent the work of many individuals over a long period of years and because they represent perhaps the most recent contribution to the perplexing problem of what determines the size of year-classes of fishes.

The first paper is concerned only with North Sea haddock. An unpublished work of possible factors governing year-class size is cited to the effect that neither variations in egg production potential nor in differential mortality after the pelagic stage of life are related to year-class size.[1]) The authors therefore reason that year-class size is determined during the pelagic phase of the life history and consider indirectly one aspect of the pelagic environment, i.e., the current system.

This paper restates the relationship between an index of North Sea haddock year-class size, developed by Thompson, Raitt, and Parrish, to water-mass movement as measured indirectly from the balance between the south-east and north-west wind resultants during the haddock spawning season in the northern North Sea. An earlier paper by Carruthers (Rapp. et Proc.-Verb., **107**, 3, 1938) presented the year-class size index as being related to the south-east wind resultant alone. The present analysis gives data on the year-class size index for the years 1920—49, exclusive of the war years 1939—44, thus adding seven years to the period of the earlier study.

A plot of the year-class size index on an annual time-scale illustrates the large variation in haddock recruitment when the fish are in their second year of life, and thereby shows one cause for variations in landings. In lieu of actual current records, the absolute (sign disregarded) difference between the north-west and south-east wind resultants are used as indicative of water-mass movement, and noted by "H":

$$H \quad \left| \sqrt{(S+E)^2 - (N+W)^2} \right|$$

[1]) A work eagerly awaited, since for one important demersal species it has been implied, if not stated, that year-class size is almost entirely a function of stock size.

where "S", "E", "N", and "W" are the four wind vectors. This wind value for the four months, February through May, is plotted against the corresponding year-class size index for the year in which the brood was spawned. With the exception of two years, 1946 and 1947, the points lie in a general upward curve, with minimum year-class size at "H" values close to zero, according to the curve drawn by the authors. The criterion under which this curve was fitted is not stated. Taking for granted that the main body of the North Sea is the only favourable nursery ground, the data bear out the interpretation given by the authors concerning transport of water from the spawning grounds to the nursery grounds as a controlling factor in year-class size of North Sea haddock.

My opinion is that although the exact position of the line drawn in the correlation figure could reasonably be altered by other investigators, the trend of the points constitutes real evidence towards the transport of pelagic haddock being a major factor in survival to the demersal-dwelling adult stage (provided, of course, that it is a *real* factor). This contribution to the knowledge of fishes supports the hypothesis advanced by many fishery workers, i. e., that the egg and larval periods are critical in the determination of year-class size in many commercial marine species. However, the fact that the relative sizes of two year-classes (1946 and 1947) do not conform to the relationship presented should serve as a reminder that the factors affecting survival during early life history are undoubtedly complex and vary from year to year. The use of a single factor, such as wind, which tends to be a kind of summation of many other factors, may lead to erroneous predictions.

A fuller account of this work is to be published elsewhere.

The second paper may be regarded as a continuation of the first; the species considered include herring, plaice, and cod. The wind functions selected by the authors correlated well, in general, with the year-class size data, suggesting that a major factor in year-class survival is related to the wind. The wind functions related to each species were different.

The philosophy underlying the interpretation of a "correlation" analysis deserves some attention. Intuitively, most workers feel some reason for hesitation in ascribing an observed correlation as causal evidence toward an hypothesis. In the case of a wind function being associated with year-class size, the complex of factors that are responsible for variation in year-class size remain unknown after the analysis is complete. Their combined effect is hypothesized to be measured by the wind function. The causal relationship, to at least some degree, must be taken for granted *before* the correlation results are proclaimed. That is, the correlation is a measure only of the degree to which the partial set of factors is useful to describe the effect of the entire set. In this case, the average water current resultants during a certain pertinent time period is the one factor being used as that which will describe the effect of all factors. If the currents and year-class size are related, the degree to which the currents do affect year-class size is measured by the correlation. However, the direct causal effect of the currents *per se* upon year-class size must be established before the correlation has any biological meaning. The mere circumstance of a correlation between the two, without previous positive knowledge of the effect of currents on year-class size, is not evidence that currents are effective. Such knowledge need not be "quantitative", however; that is, other conditions being held given, variation in currents must be *known* to affect, to some positive degree, variation in year-class size. The correlation analysis then will suggest just what that degree, with other conditions unknown, measures. Such correlations are a measure of the past association of currents

and year-class strength. Any use of these correlations or regressions to predict future association apply only if the multiplicity of direct causes maintain their past relation to each other. It is this condition, I believe, to which the authors refer when they qualify the value of their results if used for prediction.

Granted the real effect of currents upon survival of fish in the North Sea, and observing the high degree of association between measures of these two conditions, it seems obvious that the study here points out the need for a programme of study into the causal mechanics involved in the effects of wind action on year-class size. The results of such a study may uncover some more direct factor, which is even more closely associated with year-class size. There must be some intermediate factor or set of factors that affect survival more directly than, although in consequence of, the average winds or currents. The discovery of one oceanographic factor, namely currents, enables one who is concerned with more direct relationships to conduct his research from a positive point of view, and with a definite question in mind, *Why* do currents affect brood strength to such a degree? For this reason, as well as the probable value of prediction from wind conditions alone, these studies are very valuable.

T. W.

F. R. Harden Jones. "The Swim Bladder and the Vertical Movements of Teleostean Fishes."

"I. Physical Factors." Journ. Exp. Biol. **28**, 4, pp. 553—66. London, 1951.

"II. The Restriction to Rapid and Slow Movements." Ibid. **29**, 1, pp. 94—109. London, 1952.

The buoyancy of the gas in the swim bladder of a fish may provide a state of hydrostatic equilibrium at a certain depth. On any ascent above this level, the bladder distends and increases the buoyancy. The reverse will occur when movement is to a lower level. Accordingly, the gas in the swim bladder prevents the fish from reaching a stable equilibrium. Active control is permanently needed to maintain a station beyond the level of adjustment. The present investigation has been undertaken in order to determine the extent to which the distension restricts vertical movement of physoclist teleostean fishes.

The average density of the tissues being equal, a swim bladder of greater relative volume is needed in fresh water than in the sea, percentages being about 7 % and 5 % respectively.

On sudden pressure reduction, the gas in the bladder tends to expand according to Boyle's law. The expansion may be reduced either by passive resistance or by active muscular control. Apart from these physical factors, rapid vertical movements are restricted by the energy which the fish can afford to spend in order to maintain its position at the new level, while awaiting adjustment of the amount of gas in the bladder. Slow vertical movement is restricted by the rate of gas adjustment in the bladder. A mathematical formula is deduced for the time required for a certain vertical displacement. Both slow and rapid ascent and descent are included in the reasoning. The rate of gas adjustment is taken as a constant; no stress is laid on the possibility of its dependence on the deviation from the equilibrium level.

Perch (*Perca fluviatilis*) of about 10 cm. long were subjected to a pressure reduction and the volume change measured (by displacement method). The fish were then killed and the volume of the swim bladder determined (by weighing the volume of water displaced). The observed volume changes were

expressed as percentages of the original volume of the swim bladder, to be compared with those that would be obtained with a freely expanding gas. When adjusted to atmospheric pressure, the resistance to the extension of the bladder was only apparent when the pressure was reduced by more than 10 cm. of mercury.

Density changes were determined in perch (*Perca fluviatilis*), wrasse (*Crenilabrus melops*), rockling (*Onos mustela*), and dragonet (*Callionymus lyra*) when subjected to pressure reductions. This was done by measuring weight, volume, and increase of volume in reduction stages of 5 cm. of mercury. Density changes were absent in the dragonet, which has no swim bladder, and greatest in the perch, which has the largest bladder and no muscles to resist expansion.

The restriction to rapid movements was investigated in perch by studying its behaviour on sudden pressure reductions in stages of 1 cm. of mercury. Two series of experiments were made, the first with fish adapted to 0·6 m. head of water and the second with fish adapted to 6·7 m. head of water. Perch completely adapted to a certain pressure were slightly heavier than the water. When swimming in mid-water in the container, it sank slowly to the bottom and had to make compensatory movements with the fins. The time required to make 10 consecutive beats with one pectoral fin was taken as a measure of compensatory action. On reduction of pressure the beats slowed down, then took the reverse direction and became more frequent. It was found that the fish did not show any signs of discomfort at a reduction of one-sixth of the total pressure, and could still maintain its position under reduction of one-third. A reduction in depth equivalent to one-sixth of total pressure may be taken as the upper limit of rapid ascent. Further reduction made the fish restless and even excited, trying to escape downwards. This reaction in daily life prevents the fish from floating upwards in a helpless state, which might result in the rupture of the bladder at a reduction of three-fifths of the total pressure.

Restriction to slow vertical movement was investigated in two series of experiments. In the first, perch were subjected to a pressure reduction under laboratory conditions and the time required for adaptation was recorded. In another series, adaptation was observed in perch trapped at depths of 3 m. and 4·6 m. (being submitted to pressure reductions of 25 % and 33 % respectively). These observations led to an average estimate of the rate of adaptation; variations in the results were duly considered. When an initial rapid ascent of one-sixth was taken into account, a vertical displacement during 5—7 hours (as is the case in many diurnal migrations) could not involve a reduction of 40 % of the total pressure. Marine physoclist teleosts would only be able to make diurnal migrations as extensive and rapid as that shown by the so-called deep scattering layer if the swim bladder were reduced in size, the bladder wall thickened to resist expansion of gas, or the rate of gas resorption much quicker than in the perch.

J. Westenberg.

W. Stephenson. "The Lesser Rorqual in British Waters." Rep. Dove Mar. Lab., Ser. 3, No. 12, pp. 7—48, 14 figs. Newcastle, 1951.

Since August 1947 small Norwegian whalecatchers at North Shields have been landing meat from the Lesser Rorqual or Minke whale taken between Shetland and the Humber. Professor Stephenson has based his account of the biology of this whale in British waters partly on stranding records and partly on catch returns supplied by the whalers to the Norwegian Fisheries

Department or, during 1948, to him personally. He was able to obtain a small number of ovaries, some baleen plates for age studies, and a series of samples of stomach contents. There are valuable appendices reproducing full details of the whaling returns and the stranding records. About 90 strandings and 250 captures appear to be involved. There are also distribution charts which the industry should find helpful.

The facts set out in this paper are valuable but certain of the inferences, though admittedly tentative, seem open to some criticism. Examining the stranding frequencies in 10-year classes from about 1800 onwards, the author has suggested that, if population density is the main factor affecting the frequency of strandings, then there exist in the population long-term fluctuations in numbers, and there is a tendency for numbers to be increasing in recent times. Professor Stephenson's data, however, refer to reports of strandings rather than to actual strandings, so that the upward trend of his graph seems more readily explicable by the increasing attention paid to records of all kinds as the nineteenth century progressed, by the development of communications from remote coastlines, and by the rise in stranding reports to be expected after 1913 when such reporting of cetaceans was first enforced. Professor Stephenson finds evidence of age-groups in the trimodality of length frequency curves for stranded whales and for caught females, and, in support of his argument, points out that when the peak lengths of his trimodal frequencies are plotted at successive Septembers for strandings and successive Augusts for caught whales, then they lie on a smooth curve with an asymptote at 36 feet, the length at maximum growth. If this is so, then I find it puzzling that the length frequency curve for caught males is unimodal only; and it is difficult to see why the author should include both sexes in the length frequency curve for stranded whales, since he shows elsewhere that the female is longer than the male. Professor Stephenson notes however that baleen plate tracings, supplied by Professor Ruud, suggested ages greater than those derived from the length frequencies. Because of different sex ratios, differences in the proportions of pregnant females, and some size differences in the returns, the author suggests that 'the English whales may belong to a different biological group than the Scottish . . .'. This is an interesting possibility but, reviewing the data, I would say it is much more probable that the same whales are following the herring (which Professor Stephenson shows to be their principle food) from Scottish waters in July and August southward down the English North Sea coast in September and October. Rather than a theory of exclusive stocks, the observed differences can be explained by the smallness of the English sample, the likelihood of sexing errors, the likelihood of missing comparatively more foetuses off Scotland where these are younger and smaller, and the probable existence of, and progressive changes in, schooling and segregation patterns that affect the proportions in the classes of captured whales. Professor Stephenson makes some helpful observations on breeding. According to earlier authors the neonatal length is about 9 feet, and from this and an analysis of foetal lengths, the author puts the calving season in winter and mostly in November and December: the gestation period would appear to be about 8 months.

Jonsgård[1]) has recently published an independent account of the Minke off Norwegian coasts. It is unfortunate for our knowledge of Minke biology that Professor Stephenson has left Cullercoats, for otherwise consultations between these authors could have yielded profit, especially in matters of distribution. For instance, Professor Stephenson's data were

[1]) Norsk Hvalfangsttid. No. 5, May 1951, p. 209.

limited to whales captured within 100 miles of British coasts, so that his charts show virtually all whales to have been taken within the 100 fathom line: it would be interesting to know whether the species is merely coastal in summer or whether the great local width of the continental shelf in this region, and the limited range of the small diesel vessels employed, may together obscure a more oceanic extent to the summer distribution. There is the further and associated question whether English and Norwegian stocks are separate, or whether they are diverging migrational streams from a common stock whose winter residence is the temperate North Atlantic.

Robert Clarke.

Y. Hiyama. "Thermotaxis of Eel Fry in Stage of Ascending River Mouth." Japanese Journ. Ichthyol. **2**, No. 1, pp. 23—30. Tokyo, 1952.

The author tries to prove that elver migration up rivers from the sea is partly induced by thermotaxis. For this reason elvers were caught when ascending a river mouth and kept in a tank for three weeks. After this period experiments were started which lasted 5 weeks. Obviously the author assumes that during this period no change took place in the behaviour of the elvers or in their migration urge, an assumption which might have been proved first.

The experiments each consisted in putting 10 elvers into one half of a wooden tank, filled with fresh water, divided into two equal halves by a partition capable of being moved up and down. In the second half the water was kept at the same level, but at a different temperature (max. difference 4·3°C.). After the partition had been raised, elvers were counted in one half of the tank every twenty seconds over a period of 8 minutes. From the results, conclusions about thermotaxis were drawn. Let us suppose that the author is right in his statement that no water turbulence occurred, so that a distinct boundary-plane existed between the two water masses; in this situation the elvers could not perceive any change in temperature except when passing the boundary-plane, so that the results would have been influenced by the chances of their swimming. No description is given of the behaviour of the elvers when their heads and tails were in water of different temperatures, nor was the possibility investigated that elvers could become accustomed to the temperature of the storage-tank in which they had been kept.

The number of experiments was small. In four experiments elvers were put in water of about 11°C., while the other half of the tank contained cooler water. There were two positive results (the majority of elvers moving to the other half), one inconclusive, and one negative result. In one experiment elvers were put in water of about 11°C. while the other half of the tank contained warmer water. The result was inconclusive.

From these five experiments the author concludes that when the water temperature is low, viz., about 11°C., elvers prefer to migrate to cooler water.

Seventeen experiments were carried out by putting elvers in water of 14°C. or higher, while the other half of the tank contained warmer water: there were six positive, seven inconclusive and four negative results. When cooler water was used in the second half of the tank (seven weeks after the elvers had been caught), the author got one positive and eleven negative results. From this the author claims to have proved that in warm water elvers tend to swim to still warmer water.

According to the author these two tendencies can explain the upward migration of elvers from the sea into river-mouths, but in my opinion the evidence is rather doubtful.

C. L. Deelder.

I. Sörensen. "An investigation of some factors affecting the upstream migration of the eel." Inst. Freshw. Res., Rep. No. 32, pp. 128—132. Drottningholm, 1951.

This paper deals mainly with the question of the maximum speed of water against which migratory eels of different lengths can swim for a limited distance. The apparatus used consisted of a series of wooden tanks at different heights, connected with each other by channels of 1·2 m. in length. In these channels a water flow was maintained. Eeels of from 7 to 30 cm. in length were put in the lowest tank. After some hours the distribution of eels in the other upstream tanks was noted. In addition preliminary observations were carried out using a circular rotating aquarium.

It appeared that over a distance of 1·2 m., eels 7—10 cm. in length may swim against a water velocity of 0·6—0·9 m./sec.; for eels 10—15 cm. in length the maximum velocity is 0·9—1·3 m./sec.; still larger eels can swim against a velocity of 1·5 m./sec. or more. No account was taken of the period necessary to travel the given distance. Light seems to have an inactivating effect mostly on the larger eels, while low temperature appears mostly to decrease the activity of the smaller eels.

C. L. Deelder.

P. Korringa. "The shell of *Ostrea edulis* as a habitat. Observations on the epifauna of oysters living in the Oosterschelde, Holland, with some notes on polychaete worms occurring there." Arch. Néerl. Zool., **10**, pp. 32—152, 13 figs. Leiden, 1951.

Though the investigation of which this paper is a record was designed to discover a possible, though later shown to be non-existent, animal vector of shell disease, it nevertheless presents a very interesting study of the animals which have adopted the shell of *Ostrea edulis* as a habitat. At the same time it expands our knowledge of the fauna of the Dutch oyster grounds. A comprehensive list of species has been given, together with notes on breeding behaviour and useful figures for the identification of some of the more uncommon animals, particularly Polychaetes.

As the author points out, considerable attention has been devoted to bottom communities in general and oyster grounds in particular but little attention has been paid to the epifauna of the oyster itself. This fauna, at least in the locality under consideration, has proved to be surprisingly rich in both numbers and species though the reasons for the adoption of such a habitat are not immediately apparent. Experiments with live oysters and empty shells showed no significant differences in their populations so that it is unlikely that there is any relation between the feeding habits of epibionts and host. The general conclusion is that the shell of *Ostrea edulis* affords a suitable substrate for the attachment of sedentary organisms and by virtue of its scaled formation it also provides a sheltered habitat for small crevice-dwelling animals. It is probably this latter factor, coupled with the fact that the shell of the live oyster rarely becomes smothered by mud, that accounts for it supporting such a rich and varied fauna.

A great many of the animals recorded, particularly Polychaetes, are characteristic of the shell fauna but few appear to be specific to it. Comparison of the epiphytic population with bottom communities seems to indicate that there may be four or five species which occupy the habitat in preference to any other examined. Unfortunately it is not possible to be more specific. Although the author has in many cases when recording the occurrence of a

particular species on an oyster shell, also recorded its presence or absence in grab samples, under tiles etc., he has not always done so. Nevertheless it is apparent from the account that the epifauna of the oyster is noticeably different from the usual bottom fauna encountered on the Dutch grounds.

One cannot but regret, with the author, that he was unable to study the economic relationships within the ecological systems on the shells of the oyster, but in posing a variety of questions regarding this particular habitat he has provided the basis of what would be a useful subject for further investigation.

G. D. W.

Current Bibliography.

Prepared by the Editor with the Assistance of Mr. A. C. Simpson.

NOTE. The scope of the Bibliography is limited in the main to the area covered by the Council's activities, but there are included papers of general interest relating to other areas in North Temperate and Arctic regions and exceptionally elsewhere. Limnological references are not as a rule given, but papers relating to brackish waters and to salmon and freshwater fish studied by the Council are included.

Subscribers and those on the distribution list will receive regularly upon application to the General Secretary copies of the Bibliography printed on one side of the page only, for use in making up card indices.

The Editor will be glad to be advised of emendations and additions to the Bibliography.

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